FROM COLONIES TO COMMUNITIES:

NEST RELOCATION AND RESOURCE

DISCOVERY IN ANTS

by

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A dissertation submitted to the faculty of
The University of Utah
in partial fulfillment of the requirements for the degree of

Doctor of Philosophy

Department of Biology

The University of Utah

December 2013

The University of Utah Graduate School

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ABSTRACT

Ants are social organisms, likely a key behavior explaining their high ecological success. Among the benefits are enhanced foraging opportunities, group defense, and living inside nests, which help ameliorate environmental extremes. Yet sociality brings new challenges, among them a sessile life. In this dissertation I studied two crucial aspects of ants that likely evolved as a response to their sessile nature. One aspect is understanding the costs and benefits of nest relocation. To address this question, I studied the behavior of the ant *Pheidole dentata*, which is a common species of the American southeast. I found that colonies relocated often, on average every 16 days. Colonies used a variety of nest types, such as the ground, tree trunks, and under rocks. Colonies nesting in the ground were the most likely to relocate compared to other locations. Leaf-litter depth and vapor pressure deficit also increased the likelihood of colonies relocating. There were also spatial and temporal variations in relocation rates. Thus, relocation is affected by various abiotic conditions affecting colonies simultaneously. Ant nests also gave colonies a tempered environment compared to external temperature conditions. Internal nest temperatures fluctuated much less than air temperatures, and these were on average lower than external ones. Colonies appear to choose locations that remain cooler than adjacent locations. They also avoid places where temperatures will exceed 38°C, possibly because scouts are unable to forage at

those temperatures. Thus, colonies appear to have some thermoregulatory control through relocation.

A second behavior that I studied is resource discovery in ants, as the ability to find resources is crucial to their survival. In general, more ants searching for food meant faster discovery, either at the community level or at the species level. Nevertheless, the efficiency of scouts finding food differed by species. Thus, scouts of some species were able to find food faster than foragers of other species. These results highlight that discovery in ant communities depends on both the number of ants searching for food, and the individual abilities of workers at locating resources.

For Alejandra,

with all my love.

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ACKNOWLEDGMENTS

Graduate school has been an exhilarating experience. Finishing would not have been possible without the encouragement and help from so many people. I want to first of all deeply thank Don Feener, my dissertation advisor. Don was the first one to introduce me into the world of ants, and the first one to make me interested enough to slouch to the leaf-litter to look at these peculiar insects. Working in the Amazon rainforest in Peru with him has been an unforgettable experience, and the first time I got to enjoy his sarcastic and witty humor. I will be forever thankful for his thoughtfulness and help.

I would also like to thank the rest of my committee, Fred Adler, Jon Seger, Tom Kursar and Coleen Farmer. Coleen was very helpful at the start of my research by kindly allowing me into her laboratory to use her huge temperature chambers. She provided very intellectually stimulating conversations, and her ideas on ants and temperatures are fascinating. I'm sure she would be an excellent entomologist. Tom was always a positive figure during my dissertation and gave me confidence that I may finish when my confidence was lacking. Jon has been a great inspiration. I always enjoyed his intellectual thoroughness and the great conversations that he stimulated. The suggestions that he gave for my dissertation have been extremely valuable. Fred has been not only a great mentor on statistics, but the center of intellectual curiosity, discussion and enjoyable conversations on the insect-side of things at the department.

I would like to thank Jack Longino for providing a friendly atmosphere while hosting the ant-group meetings. His work in the tropics and his scientific outreach have long been an inspiration for me. Shannon Nielson made my graduation possible by remembering all those deadlines that I always forgot, and simply by being such a wonderful person. Thank you so much!!

Graduate school would not have been the same without my lab-mates. I shared a short time with Elliot Wilkinson, but he always seemed a positive guy. Jessica Pearce has been a great friend since I first met her in a warm summer day at SWRS, Arizona. I've always enjoyed her company and intelligence, and look forward to enjoying her company before too long. Phil Wiescher has become a good friend, and I've enjoyed his humor and letting him win during our racquetball games. With Roxana Arauco, I've shared lots of good conversations, and we've become good friends. Arne Hultquist always brought his great uplifting energy to the lab and gave us adventurous river trips. Outside of the lab, I want to thank Jose Crespo, for being a great person, and a good friend. Luciano Valenzuela, Carina Maron, Georgia Sinambu, Maria Jose Endara and the rest of the Latinos have made life in Salt Lake very enjoyable.

Several undergraduate volunteers helped me throughout my dissertation. I want to especially acknowledge Anthony Ho for his courageous field work in Austin, Texas. His help was invaluable for collecting large amounts of data during hot summer afternoons. John Hintze, Dallin Ashby and Dan Davis all helped in the lab.

I would like to thank the staff at Brackenridge Field Laboratory and Stengl Lost Pines for their help and opening their facilities for my research. Special thanks goes to Larry Gilbert, John Crutchfield and Steve Gibson.

My family, of course, deserves special thanks. Sylvia Torti was always an inspiring cousin throughout my life. Becoming a biologist has been in a large part thanks to her enthusiasm and encouragement. My parents, Marisa and Marcelo, sparked my interest in the world around me and in the world of ideas. They showed me that you can look at the world with the eyes and wonder of a child while being an "adult." My brothers, Diego and Fernando, always encouraged me to finish and have given me their companionship and friendship.

And last, but not least, I want to give my thanks to the love of my life, my wife Alejandra Gutierrez. She has been my sunlight and starlight since I met her, and it is thanks to her love, compassion and patience that I have finished. She has believed in me during my moments of self-doubt, and has been my motivation for reaching this finish line. This dissertation is for you.

CHAPTER 1

INTRODUCTION

From Latreille's (1799) early taxonomic studies, to Darwin's exploration of natural selection on the evolution of eusociality in ants (Darwin 1859), and Wheeler's (1910) seminal book "Ants," the Formicidae have fascinated numerous researchers throughout the centuries. Because of their social organization and abundance in most terrestrial ecosystems, ants make ideal organisms for studying a variety of biological questions (Hölldobler and Wilson 1990). Ants can be studied at the level of the individual, the colony, or the community, as the rules and environmental factors that govern each level of organization are different. Ants have been extraordinarily successful at dominating many terrestrial environments, either in terms of the biomass that they represent in ecosystems, or in terms of the number of interactions with other species of their communities (Wilson 1971, 1990). Ants play several keystone roles in ecosystems (Wilson and Holldobler 2005), acting as predators (Franks and Bossert 1983), herbivores, seed harvesters (Hölldobler and Wilson 1990), and soil engineers (Folgarait 1998). Ants have also mastered the agriculture of fungi, herding and milking of other insects, communal nest weaving, cooperative hunting in packs, social parasitism and slave making (Hölldobler and Wilson 1990, Brady et al. 2006). They represent a much greater proportion of insect biomass than what their biodiversity alone

would suggest. In the Amazon rainforest, for instance, ants can comprise up to four times the biomass of all land vertebrates (Fittkau and Klinge 1973). This success is likely due to numerous advantages that come from being eusocial (Wilson 1990), among them the ability of different workers to perform multiple tasks simultaneously, like defend nests from predators and food from competitors, tend to the immature larvae, and repair the nest when it is damaged; what Wilson calls series-parallel operations (Wilson 1990, Hölldobler and Wilson 1990). But also, and unlike many solitary insect species, ants are able to control the abiotic conditions inside nests (Jones and Oldroyd 2006). The advantage of nesting in the soil or cavities is the protection provided by the nest against high and low temperature extremes, rain or wind. Further, because the queen inhabits the innermost sections of the nest, the colony is more likely to survive as long as she stays alive.

Sociality also enables greater foraging opportunities for ants. Because workers are sterile, they can avoid trade-offs associated with expending energy in reproductive organs or in finding mates (Traniello 1989). Through natural selection workers are likely to have become efficient at maximizing energy intake and minimizing time costs while foraging. For example, ants have evolved several mechanisms that increase the range of food sizes available to the colony. One of these is the ability to lay down pheromone trails and communicate the location of food resources to nest mates (Wilson 1971). Many species are also able to mass recruit to these resources and protect them from competitors. If the food item is too large to be transported back to the nest in one piece, workers can cut portions and bring the food individually or in groups (Holldobler

and Wilson 1990). These behaviors allow ants to gather food that would be unavailable to other solitary foraging insects.

Although sociality brings many benefits to ants, there are also a number of challenges that must be solved that are a product of coloniality and their nest building. First, colonies typically live protected inside nests, which can require a substantial amount of investment in time and energy to build. Yet it has become increasingly clear that ants are not sessile in the true sense of the word: colonies of many different species repeatedly relocate nest locations (McGlynn 2012). What is poorly understood is if there is a common underlying thread behind nest relocation in ants. Relocation is widespread phylogenetically and geographically. There is a wide degree in the frequency of occurrences, from species that are truly nomadic, such as army ants, to species that rarely move, such as neotropical leaf-cutting ants of the genus *Atta*.

Nest size appears to play an important role in the frequency of nest relocation. Twig-dwelling species in a neotropical forest, for example, move often, between every 35 to 146 days (Byrne 1994). This high frequency could be due to the fact that nests located in between leaf-litter or in hollowed twigs are ephemeral by nature and might need to be abandoned when internal conditions deteriorate (Byrne 1994, Kaspari 1996). Yet even species whitch construct larger nests, such as seed-harvester ants of the genus *Pogonomyrmex* and *Messor* also relocate, although less often than leaf-litter ants (Gordon 1992, Brown 1999).

What appears to underlie the frequency of nest relocation in different species is the investment, in terms of time and energy, of constructing the nest. For example, army ants of the genus *Eciton* relocate nearly every day during their nomadic phase, as the

colony collects food to feed the adults and their larvae (Schneirla 1971, Franks 1983). Peculiar to army ants is that colonies do not construct any permanent nests; they rather aggregate into a "ball" of ants known as a bivouac. This strategy likely reduces the costs of nomadism significantly. For species that construct large nests, and thereby invest greatly into making their living quarters, the costs are likely too high to justify frequent relocations.

Although nest relocation appears to be an adaptation that allows colonies to alleviate their sessile nature, our understanding of the specific causes behind relocation remain nebulous (McGlynn 2012). The deterioration of nest habitats in twig-dwellers (Byrne 1994), or the abandonment of nests when invaded by predatory ants (Smallwood and Culver 1979, Droual and Topoff 1981, Dahbi et al. 2008) are of the few cases where nest movement can be tied to particular conditions. In most researched species, however, the events triggering relocation are not at all obvious. In the harvester ants *Pogonomyrmex barbatus* and *Messor andrei,* relocation does not appear to be the result of army ant attacks or changes in microclimate, nor competition with neighboring colonies (Gordon 1992, Brown 1999). Nevertheless, Gordon (1992) suggests that colonies might move repeatedly because they carry some disease.

In order to address the paucity of information on relocation in ants, I chose to study the ant *Pheidole dentata*, a species native to the American southeast. This ant seamed well suited to study relocation, as anecdotal evidence by D. Feener suggested that it moved frequently. This species nests in a variety of substrates, such under rocks, in the leaf-litter, and in wood, so it was an opportunity to test nest preferences and the effects of location on relocation rates. In addition, *P. dentata* is attacked by a

specialized phorid fly parasitoid, *Apocephalus feeneri* (Feener 1981). *Apocephalus feeneri* attacks the soldier subcaste of *P. dentata* while foraging outside the nest. If the attack on a soldier is successful it results in the eventual killing of the soldier by the parasitoid larva. These phorid flies can also harm a colony by disrupting its foraging trails, as workers commonly retreat back to the nest while attacked by flies. As a result, workers are more likely to lose the control of food resources to other species. The interaction of *P. dentata* with its parasitoid fly allowed me to study if nest relocation was a response to escape these phorid fly attacks.

I found that colonies in fact relocated often, on average every 16 days. Several abiotic factors increased the chances of relocation, such as colonies nesting in the ground, higher leaf-litter over nests, or high air vapor pressure deficit. There were also temporal and spatial effects affecting relocation chances. Nevertheless, the abundance of phorid flies did not change the likelihood of colonies moving. In terms of explaining the frequent relocations of *P. dentata*, my research paints a complex picture. As in other studies, relocation does not seem be a result of reduced resources or to avoid competition, because colonies moved short distances. Relocation could be triggered when a particular set of environmental conditions are met, or colonies could be moving because of some other unknown reason, such as nest pathogens, or predators, such as army ants.

In Chapter 3 I further examine the significance of nest relocation by studying whether *P. dentata* colonies use this behavior to find better microclimates. Thermoregulation as a colony behavior is common in social insects, and one of the most crucial innovations of social insects (Jones and Oldroyd 2006, Hölldobler and Wilson

2009). Temperature control of nests allows ants to stay active even when it is either too cold or too hot for solitary species to forage (Wilson 1990). Nevertheless, most research on thermoregulatory behavior in ants has focused on the ability of colonies to increase their nest temperature. For example, several wood ant species of northern temperate forests of Europe are able to generate heat from bacterial metabolism and the workers themselves to keep the brood warm (Coenen-Stass et al. 1980, Rosengren et al. 1987). In species with small colony sizes, they may increase nest temperatures by relocating to locations with higher insolation (Smallwood 1982). But the behavior of colonies in hot environments is less well known. Would ants still prefer to increase insolation to increase nest temperatures, or would colonies show evidence of heat avoidance?

Summers in Texas can be extremely hot; soil surface temperatures can exceed 50°C, while air temperatures can frequently approach 38°C. Given that *P. dentata* inhabits mainly soil habitats, colonies are more likely to encounter situations of heat-related, rather than cold-related, stress. Extreme high temperatures could affect ants inside nests if these became too warm, or they could hinder successful foraging if external temperatures were too hot for ants to leave the nest. Recent research has shown that recruitment pheromones of ants are volatile, and that the rate of volatilization increases with soil temperatures (van Oudenhove et al. 2011). Thus, the location of nest sites could be a crucial factor determining the success of a colony. *Pheidole dentata* colonies are an ideal study system to address thermoregulation. Because they relocate often, temperature could be one factor taken into account while deciding nesting locations.

I found that, in fact, *P. dentata* colonies seem to thermoregulate by selecting locations that are cooler than the general environment. Temperatures inside nests were cooler than external air temperatures, and fluctuated less. But importantly, colonies avoided nesting in locations where the soil temperature exceeded 38°C. This is significant because 38°C is the maximum foraging temperature of *P. dentata* (Wiescher et al. 2011). If nests were placed in locations where the soil exceeded 38°C, it might limit the window of foraging opportunity of colonies as foragers would be unable to leave the nest. This is one of the first studies showing that nest location might be limited by warm temperatures in hot climates. Certainly more research is needed to understand the effects of high temperatures on the foraging success of *P. dentata* colonies and its effects on fitness.

There is a second fundamental trade-off that ants confront arising from their sociality. In the process of becoming social, ants adapted to living in nests, which provided colonies with stable environmental conditions. But by doing so, colonies traded-off their ability to forage freely (as solitary insects might do) by becoming central placed foragers: i.e., all the food collected by workers is brought back to the nest to feed the coworkers, the brood and the queen. Central-place foraging restricts the potential foraging area of a colony, as scouts and foragers must eventually return to the location from which they began foraging. Thus, colonies could become energy restricted, either because their location could be resource-poor, or because of intense competition from neighboring colonies (Traniello and Levings 1986).

Species are likely to have had intense evolutionary pressure to locate food resources quickly, or at least to exploit the resources once found. In fact, the energy

intake of colonies appears to be more limited by the amount of foraging time than by the energy costs invested by foragers during food search and retrieval to the nest (Fewell 1988, Weier and Feener 1995). Although it is likely that all ant species have had the same driving pressure to reduce time and energy costs while increasing energy intake (Bailey and Polis 1987, Naug and Wenzel 2006), the foraging strategies used by different species to accomplish this are diverse (Traniello 1989), and the outcome has been a variation in discovery times or dominance ability of species.

Ant communities present us with a conundrum. As with many plant communities, species follow a dominance hierarchy, with the most dominant species able to exclude less dominant species from food resources, and this hierarchy is strictly linear. There is also abundant evidence that species compete strongly and directly for nest sites and food resources (Savolainen et al. 1989, Hölldobler and Wilson 1990). Without any compensatory mechanism, this situation would lead to a "Hutchinsonian demon," a hypothetical ant species able to appropriate all resources and drive all other competitors to extinction (Kneitel and Chase 2004). But, as mentioned above, ant communities are diverse, so clearly a mechanism is allowing subordinate species to coexist with the more dominant ones.

Several trade-offs have been proposed to explain coexistence in ant communities. All these trade-offs refer to the dominance ability of species with respect to other traits, such as dominance-thermal vulnerability trade-off (Cerdá et al. 1997, Cerdá et al. 1998, Bestelmeyer 2000), dominance-parasitoid vulnerability trade-off (Feener 2000, LeBrun 2003, Feener et al. 2008) and the dominance-discovery trade-off (Vepsäläinen and Pisarski 1982, Fellers 1987, Holway 1999, Lebrun and Feener 2007,

Feener et al. 2008). In this dissertation I focused on the dominance-discovery trade off, which has been found to occur in many different habitats (Cerdá et al. 2013). In this trade-off, species fall along a continuum between being good at dominating food resources and being good at discovering them.

There are two reasons that can explain this trade-off: the first arises from the fact that workers can fall into two mutually exclusive behavioral casts: they can either act as scouts, which leave the nest in search for food and return to the nest to communicate a food discovery to the nest mates, and foragers, who harvest and defend the food discovered by scouts and remain in the nest until a discovery is made (Johnson et al. 1987, Davidson 1998, Feener 2000). The second reason comes from a colony having a finite number of workers; thus, it could potentially invest in a large number of scouts, which would allow it to find food quickly, or in a large number of recruits, which would allow the colony to dominate food resources from other species but find food less quickly.

The majority of research into the dominance-discovery trade-off has focused on studying the dominant behavior of ants, and much less is understood about the sources of species-specific differences in discovery ability. In Chapter 4, I address resource discovery in ant communities and study whether species in fact differ in their ability to discover resources and through which mechanisms those differences occur. In order to generalize these findings, I studied three communities of Spain, which had a number of species unique to each location, and a number of species shared by all three. This allowed me to investigate the differences in discovery ability in more detail by studying how shared species behaved in each different location. It also allowed me to compare

discovery in Spain with research recently conducted in Texas and Arizona by J. M. Pearce-Duvet (2010, 2011a, 2011b).

I found that discovery success of a species depended on two characteristics. For the majority of species, more scouts searching for food meant faster discovery time. This had been hypothesized to occur in ants (Johnson et al. 1987), but had never been tested outside of North America (Pearce-Duvet et al. 2011b). Perhaps more interestingly, scouts of different species differed in their individual ability to discover food. I found that species with the best discoverers in all three communities were also the least dominant species. The results also suggest that fast discovering species may be setting the pace of discovery at the community level, as suggested by previous theoretical work (Adler et al. 2007). Finally, two species which were fast discoverers were also temperature generalists, able to forage even when soil temperatures were too warm for foragers of other species.

These results provide some answers to our conundrum. Although ant communities are organized into transitive dominant hierarchies, species also differ in their ability to discover food. Although most species were able to rely on the number of scouts to reduce time to discovery, apparently not all scouts are created equal. Some species could rely on a smaller number of efficient scouts which could withstand higher temperatures to find food. Perhaps these differences between species, which run on several behavioral and physiological axes, are able to explain coexistence in these communities. Although it is necessary to further explore ant communities, this chapter certainly places us closer to understanding species coexistence in temperate communities.

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CHAPTER 2

NEST RELOCATION IN THE ANT *PHEIDOLE DENTATA* (HYMENOPTERA: FORMICIDAE)

Abstract

We studied nest relocation in the ant *Pheidole dentata*, a common species in the southern United States, by following colonies for 6 weeks. We correlated probability of relocation with several abiotic and biotic environmental factors, such as air temperature, humidity, leaf litter depth (LLD), nest type and presence of phorid fly parasitoids. Colonies moved often, on average every 16.2 days. By the end of our study, fewer than 5% of colonies marked at the start remained in their original nests. Only 3.1% of colonies returned to a previously used nest. The mean distance of relocation was 0.76 ± 0.73 m. Colonies nested in a variety of locations, such as in the ground, by tree trunks, under rocks and inside wood. Several factors affected probability of relocation. Higher LLD and vapor pressure deficit increased probability of relocation. Chance of relocation varied by nest type, by plot and week of study. We found no evidence that surface cover or rain affected relocation behavior. Colonies appear to avoid nests that become dry by nesting against tree trunks. Phorid fly abundance had no effect on colonies chances of relocation. Colonies appear to live under a trade-off between higher LLD used as

protection against heat, and increased habitat complexity in a high LLD environment. We discuss other implications of frequent nest relocations.

Introduction

Ants are regularly compared to plants because these groups share many common life history traits (Andersen 1991, López et al. 1994, Andersen 1995). Both types of organisms experience modular growth (López et al. 1994) with leaves and roots "foraging" for food in plants and the sterile worker caste foraging for food in ants. At the community level, interspecific competition shapes both plants and ants (Tilman 1990, Adler et al. 2007). Also, the way plant communities are structured into "dominant" and "subordinate" species finds a parallel in ant communities, whose species can also be ranked by their degree of ecological or behavioral dominance (Tilman 1990, Feener 2000). However, the common perception that ant colonies are fixed in place (sessile) like plants is now being challenged by the realization that many, if not most, ant species have the capacity to relocate nests (summarized by McGlynn 2012). This emerging picture shows that nest relocation not only happens in ants, but also in the other social insects, such as bees (Dyer and Seeley 1991, Itioka et al. 2001), wasps (Hunt et al. 1999) and termites (Noirot et al. 1986, Rupf and Roisin 2008).

The diversity of ant species that relocate is high, and is widespread with respect to geography, colony size and life history. For example, relocation behavior has been documented in Central American rainforests (Byrne 1994, McGlynn et al. 2003), in temperate woodlands of North America (Smallwood and Culver 1979b, Droual and Topoff 1981a, Gordon 1992), Europe (Buschinger 2010) and Japan (Tsuji 1988), in old

world tropics (Maschwitz and Hänel 1985) and Australian deserts (Schultheiss and Cheng 2011).

Relocation also occurs in both large and small colonies (Smallwood 1982b, Maschwitz and Schönegge 1983, Gordon 1992, Byrne 1994, Freitas 1995, McGlynn et al. 2003). Also, species with very different life histories relocate, such as seed harvester ants (Van Pelt 1976, Gordon 1992, Brown 1999), specialized predators (Schneirla 1971, Maschwitz and Schönegge 1983, Freitas 1995), and generalist omnivores (Smallwood and Culver 1979b, Smallwood 1982b, Byrne 1994, Banschbach and Herbers 1999, McGlynn et al. 2003, McGlynn et al. 2004). Many invasive ant species are characterized by being polydomous, with frequent migration between nest sites (Hölldobler and Wilson 1977, Clark et al. 1982, Holway and Case 2000, Heller and Gordon 2006, Debout et al. 2007).

The ubiquity of relocation behavior in ants suggests that it must confer some ecological or evolutionary advantage to the colony, despite potential costs, such as loss of foraging time, predation and increased mortality risks while migrating. Nest sites are crucial to ant ecology because they enable colonies to maintain homeostasis by way of thermoregulation and the control of relative humidity inside the nest (Wilson 1971, Jones and Oldroyd 2006). Nest sites also provide protection against predators and parasites (Hölldobler and Wilson 1990), although it is conceivable that nest sites might also act as attractants to predators and parasites. The location of colonies with respect to the same or other species could also determine the degree of competition that ants might encounter (Smallwood 1982b). Therefore the spatial position of the colony is likely a

key determinant of a colony's fitness, but with a few exceptions, the purpose of nest relocations is not well understood.

Do colonies move nests because of some detrimental factor inside the nest, or do they relocate because the colony is able to take advantage of better conditions elsewhere? For many species, it has been difficult to connect nest relocation to ecological or evolutionary benefits. Perhaps the most iconic example of colony nomadism, and the most understood, is illustrated by army ant colonies, whose relocations are believed to be an adaptation to avoid resource limitations that arise from their predatory feeding behaviors (Wilson 1971, Franks and Fletcher 1983).

Nest relocations of *Pheidole desertorum* and *Pheidole hyatti* provide another explanation of the role of emigration. These two *Pheidole* species maintain several nesting sites simultaneously, but only one site is used at a time. When workers detect the presence of army ants of genus *Neivamyrmex* in the vicinity of the nest, they trigger a nest evacuation and the colony regroups at alternate nesting sites (Droual and Topoff 1981b, Droual 1984). Likewise, McGlynn (2010) provides evidence that the frequent relocation of the Central American ant, *Aphaenogaster araneoides*, is a strategy to reduce the accumulation of colony odor at the nest site, which might interfere with the workers' ability to detect the odor of arriving army ant raids (McGlynn 2007). Although predation by army ant species can drive their ant prey to relocate nests, predation pressures cannot explain ant relocation in regions where no army ants are present, such as in the cold temperate regions of North America, Europe and Asia.

There is little evidence that inter- or intraspecific competition drives relocation (Gordon and Kulig 1998, Brown 1999, McGlynn et al. 2004, McGlynn 2012).

Numerous authors have suggested that ants might be responding to resource depletion (Freitas 1995), microclimatic changes (Carlson and Gentry 1973, Smallwood 1982a), or escaping from parasites and pathogens (Smallwood and Culver 1979b, Gordon 1992, McGlynn et al. 2004, McGlynn 2007) when relocating.

In this study we report on the relocation behavior of *Pheidole dentata*, a dominant member of the ant community of the southern United States. Our interest in *P. dentata* originates from several traits that we believe make this species particularly useful for understanding nest relocation in ants: 1) Colonies have been observed to relocate periodically, especially after the nest site was disturbed (D. H. Feener, Jr., pers. obs.). 2) Colonies nest in a variety of microhabitats, such as in leaf litter, under rocks, in logs, etc. 3) Colonies do not appear to invest heavily in nest structure, as little excavation is observed at nest sites. 4) Foraging trails are routinely attacked by parasitoid phorid flies (Diptera: Phoridae) that oviposit on the major workers (Feener 1981a), and colonies might have strong incentives to emigrate to reduce phorid fly attacks. In our study we aimed to understand the effects of these traits on *P. dentata's* nest relocation behavior.

Materials and Methods

Study Site

We conducted our research at Brackenridge Field Laboratory (latitude ~ 30°17'N, longitude ~ 97°46'W, elevation ~ 145 m), in Austin, Texas, during the months of May through July of 2008. The vegetation consists of a mixed juniper-oak forest, mainly *Juniperus ashei* (Post Cedar, Ashe Juniper), *Taxodium distichum* (Bald

Cypress), *Ulmus crassifolia* (Cedar Elm), and *Quercus fusiformes* (Live Oak). The average annual rainfall is 854.71 mm, with rain distributed evenly throughout the year. The hottest month is August, with a mean temperature of 28.9 °C, and the coldest month is January with a mean of 9.3 °C.

Experimental Design

We established 6 plots of approximately 50 m x 50 m and followed colonies in these plots through time. Three plots were set in open forest and three were in more closed, shaded forest. Plots were at least 100 m from each other.

Pheidole dentata colonies are monodomous and monogynous (M. Moyano, per. obs.), and their nests have a small inconspicuous entrance. Nests were located by placing pecan cookies on a plastic card every 10 m, and ants carrying cookies were followed back to their nests. Nests were marked with a survey flag, and labeled with a unique code for identification, allowing us to track the colonies through time and through different nest sites. In each plot roughly 30 *P. dentata* nests were initially marked.

One plot was censused per day, except plots Br 4 and Br 3, which were censused on the same day; each plot was censused on a weekly basis. In order to check if a nest that had been active the week before was still occupied, bits of pecan cookies were left at the opening of the nest at the beginning of every census. If no ant activity was observed at a nest site after 15 minutes, we assumed it had been abandoned. If the colony had relocated, we attempted to locate its new nest site by setting 4 cookie baits 1.5 m from the abandoned nest site.

Initial observations indicated that relocation distances were often short. We typically inferred a colony's new nest site because only a single new inhabited site was found near the old vacant site. When the colony was found in a new nest site, it was marked with a new flag and labeled with the same colony ID but with a new nest code. The distance between the new and old nest sites was measured.

When a new occupied nest site was found more than 8 m from the old vacant nest site, or if two or more active nests were found after a nest had been abandoned, we made no assumptions about the identities of the new nests: the old colony was considered to have been lost and the new colonies were added to the census for future tracking.

Nests were classified into five categories: 1) ground – for colonies nesting in the soil or leaf litter; 2) tree trunk – for colonies nesting between the soil and the roots of trees; 3) rock – for colonies living in rock cracks or underneath rocks; 4) inside wood – for colonies that live inside twigs or fallen branches in the ground; and 5) other – any other nest type.

Percent Cover and Leaf Litter Depth

Because some nest sites were subjected to high solar insolation, which could affect temperature and relocation patterns, we measured the percent surface cover over the active nests and leaf litter depth. Since the focus was to investigate objects that provided shade at smaller (nest-size) scale, the cover provided by higher vegetation (such as trees) was not estimated. Surface cover was estimated using a 0.5 m x 0.5 m quadrat, which was divided into four equal-sized squares and placed over the nest

entrance. The amount of cover provided by low lying grass, wood and rock, as well as uncovered ground, was estimated using a 1 to 6 scale, 1 being 0 % cover, and 6 being 100% cover. Leaf litter depth was measured at every nest site by averaging four measurements, one from each of the squares of the quadrat. If an object such as a tree trunk occupied part of the quadrat's area, leaf litter depth was estimated only from the unoccupied squares.

Air Temperature and Humidity Recordings

Air temperature (T) and relative humidity (RH) were measured throughout our study season with 4 Hobo H8 Pro Series loggers (Onset Computer Corporation, Bourne, MA, USA), placed at the center of each of four randomly chosen plots. Loggers recorded ambient temperature and relative humidity every 10 minutes; their data was later aggregated into a single "BFL dataset." From this dataset all measurements from a particular hour of the day were averaged, which resulted in 24 1-hour averages of T and RH per day. To simplify analysis, we assumed that all 6 plots had the same T and RH.

Abiotic Environmental Factors

We studied the role of three abiotic environmental factors (AEF), 1) temperature; 2) relative humidity and 3) water vapor pressure deficit (VPD), by analyzing their effects on the probability of colony relocation. We used the calculated 1-hour averages of temperature (T) and relative humidity (RH), (obtained from the "BFL dataset"), to calculate values of VPD (Campbell and Norman 1998), where

$$VP_{\text{sat}} = 0.6108 \exp\left(\frac{17.27\ T}{T + 237.3}\right),$$

$$VP_{\text{air}} = VP_{\text{sat}} \frac{\text{RH}}{100}$$

and

$$VPD = VP_{\text{sat}} - VP_{\text{air}}$$

VP_{sat} is vapor pressure of saturated air; VP_{air} is the partial pressure of water in the air. *VPD* (measured in kPa) is a measure of the drying potential of the atmosphere and of the desiccation risk of ants (Lighton and Feener 1989, Kaspari 1993). If colonies are sensitive to abiotic factors, they could potentially respond to factors that persisted for longer periods of times, such as several days of hot, sunny and dry conditions. In this case the use of the multiday average of this particular AEF (such as temperature) might be better at explaining the probability of relocation. Alternatively, colonies could be affected by short-term extremes, such as a particular day with high temperature and low humidity. In this case, using the respective maximum or minimum values would show greater explanatory power. Because the censuses were done approximately every 7 days, any extremely low or high value in the 6 days between censuses could have prompted colonies to relocate. Then again, the average value of the AEF for the 6 days in between censuses might have better explanatory power. To distinguish among these different scenarios, we ran our analyses with a) the highest 1-hour AEF value for the 6-day period, between-census days; b) the lowest 1-hour AEF value for the 6-day period, between-census days, and c) the average AEF value the for 6-day period, between-census days (see Table 2.1 for the complete list of AEF).

In addition to AEF based on temperature, humidity and *VPD*, we studied whether rain increased the likelihood of relocation by adding the total precipitation (in

mm) that occurred in between two censuses. Rain was added as a covariate to the main model.

Effect of Phorid Flies on Colony Relocation

The phorid fly *Apocephalus feeneri* is a specialized parasitioid of *Pheidole dentata*, which reduces *P. dentata's* ecological success against competing ant species (Feener 1981b, Disney 1982). To determine whether *P. dentata* colonies are more likely to abandon nests with high phorid densities, we counted the number of phorid flies observed at colony nest sites during each census. To count phorid numbers, we placed pecan cookie crumbs at the nest entrance of an active colony to initiate nestmate recruitment. Phorid flies were counted approximately 30 minutes after the first foragers were observed. Phorid fly density potentially impacts a colony's relocation decision proactively, therefore we used phorid density as a covariate for explaining nest relocation events of the census 1 week after the phorid fly count. For example, we tested the effect of phorid density at week 1 on the relocation probability of nests at week 2.

Statistical Analysis

We carried out 3 different statistical analyses using R 2.13 (R Development Core Team 2011). First, in "probability of nest relocation" analysis (NR) we quantified the chances of nest relocation using a binomial generalized linear model, given that the nature of our data was that a colony had relocated (1) or not (0) on a given census. Because most colonies were censused multiple times, we carried out a generalized

linear mixed model using glmmML (glmmML Package for R) to control for the non-independence of data. We used colony ID as a random factor in this analysis, which allowed us to control for any possible autocorrelation of the relocation probability within colonies.

We included 20 covariates in the NR model (Table 2.1): plot, week of census (weeks 1 to 6 used as factors, to control for any possible variation associated with the week in which a census was carried out), ground cover, leaf-litter depth of nest, nest type, infrared surface temperature of nest, and 10 abiotic environmental factors: rain (mm), and maximum, minimum and average of 1) air temperature, 2) relative humidity and 3) *VPD*. Covariates were first assessed by running each explanatory variable separately against relocation events. All the significant covariates were later used in a complete model. The complete model was then reduced via backward elimination and the best model judged based on Akaike's Information Criteria (AIC).

Second, a separate glmmML model was carried out to study the effects of phorid flies on nest relocation. In this model the number of phorid flies was run against relocation events of the week following the phorid fly count. This model was run in the absence of other variables (Table 2.1) as the small sample size was smaller than nest relocation data.

Third, a parametric survival analysis (SUR) was used to estimate the average duration of colonies at nest sites. In our data, the duration of a colony in a nest can be thought of as a time-to-event data, with the event being colony relocation. Parametric survival analysis provides estimates of parameter values, unlike the semiparametric Cox proportional-hazards models, which give parameter values with respect to a baseline

(Therneau and Grambsch 2000). We assumed that the data followed a negative exponential, with a constant decay rate μ; the average time-to-event was obtained from the reciprocal, $1/\mu$. We did not include covariates in this analysis as we were only interested in a mean estimation of μ.

Results

Colony Movement

In this 6 week study we found 212 ant colonies. They inhabited a total of 445 nest sites (an average of 2.1 nests per colony). As new colonies were found and added to the census, the number of colonies being censused every week increased throughout the study period.

Colonies moved often, having an average decay rate $\mu = 0.43$, equivalent to 2.31 weeks (average) per nest site, which corresponds to 16.2 days per site ($n = 517$, 95% *CI* = 14.75 to 17.85 days; Figure 2.1). By the end of the study, less than 5% of the colonies censused in week 1 were still in their original nest sites. The average number of relocations per colony was 2.0 and ranged from 0 to 6, although this maximum could be an underestimate if more than one relocation event occurred in between our census days. If this were the case, the actual occupancy half-life might be shorter than the 16.2 days that we documented here. Very few colonies moved to nest sites which they had previously occupied: of the 416 documented colony movements, only 13 (3.1%) relocations occurred to a site used before by that same colony.

Relocation distances ranged from 0.15 m, to 3.54 m, and the mean moving distance was 0.76 m ± 0.73 m (*SE*). Relocation distances were shorter than foraging distances, which can reach up to 3.00 m. A colony's moving distance was independent

of any of our studied factors ($F_{(25, 308)} = 1.393$, $P = 0.1037$), which suggests that distance of relocation is likely dependent on the availability of adequate nesting sites.

In approximately 384 hours of field work, two relocation events were directly observed. The first was on plot Br 1 at 4:00 pm, 07-June-2008. The second occurred on plot TX3 at 6:18 pm, 01-July-2008. Throughout both events, minor and major workers walked along a trail on the leaf-litter's surface. Only minors were observed carrying brood and the queen was guided by a dense group of workers, which sometimes dragged her by the antennae. Ants entered their new nest site through an inconspicuous hole in the leaf litter. No digging was observed at either nest site that indicated construction of their nest. The relocation distance on the June 7 event was not recorded. On July 1, the colony moved at least 3 m to its new nest site, but the abandoned nest could not be located to measure total relocation distance. Both events lasted between 15 to 20 minutes. On the July 1 event, 3 phorid flies were observed hovering above the relocation trail of the colony, attempting to oviposit on the major subcaste, although no oviposition attempts were observed against the queen.

Nest Site Characteristics

P. dentata is a nesting generalist within woodland habitats and therefore uses many of the available resources in the environment for its nesting needs, such as the soil, tree trunks, beneath rocks and in rotten wood. It was nonetheless mostly absent from short-lived locations like twigs or on the surface of the leaf litter (Figure 2.2). Of the recorded nest sites ($n = 445$), 231 (46.1%) were located in the soil (either with or without leaf-litter), but a significant number of colonies nested by standing tree trunks

or under fallen logs (28.3%), or had nests inside rock cracks or underneath stones (19.8%). Only 5.8% of the sites were found in more ephemeral places (e.g., inside dead twigs). Colonies were never observed nesting in non-forested areas with high solar insolation, which tended to be occupied by more heat-tolerant species such as *Pheidole bicarinata, Monomorium minimum* and the red-imported fire ant, *Solenopsis invicta*.

Most nest sites had little surface cover. On average only 28% of a nest area was shaded by herbaceous plants, dead wood or rocks (Figure. 2.3), even though grasses and herbs were abundant on the forest floor (M. Moyano, pers. obs.). Average leaf litter depth (LLD) of nest sites was 3.8 cm (range = 0 to 10.2 cm, n = 445, SE = 1.9 cm). Leaf litter depth of nest sites varied significantly by plot ($F_{(5, 418)} = 9.225$, $P < 0.0001$) and nest type ($F_{(4, 418)} = 2.588$, $P = 0.0364$). There was no significant interaction between nest type and plot ($F_{(17, 418)} = 1.605$, $P = 0.0595$; Table 2.2)

Biology of Nest Movement

The chances of relocation for a colony depended on the plot where it was located, on the week of our study, on nest type, on leaf litter depth at the nest site, and on the average VPD of the week previous to the census (Average Mobile VPD). In our analysis, the intercept (the value upon which all other factor levels are compared) corresponds to levels “Br 1 + Br 2 + TX3” for factor Plots, weeks “1 + 2 + 6” for factor Week, nest type “ground” for factor Nest Type, plus values of zero cm of leaf-litter depth and zero VPD (Table 2.3). Colonies located on plot levels “Br 3” and “Br 4 + TX1” had significantly lower relocation odd ratios compared to the intercept; thus, the proportional change in odds (odds ratio) of relocation for a colony in plot level “Br 3”

were exp (−0.9047) = 0.405 (Table 2.3), less than half the odds with respect to the intercept; the odds for plot level "Br 4 + TX1" were exp (−0.4776) = 0.620, or 62% of the odds of the intercept.

During weeks 3 and 4 colonies were less likely to relocate (odds ratio = 0.594 and 0.387, respectively) and during week 5, the odds were almost 3 times higher that a colony would relocate (2.926), compared to week level "1, 2, 6."

Higher leaf-litter depth increased relocation probabilities. Every cm increase of leaf-litter depth raised the chances of a colony moving by 12.3% (odds ratio = 1.123, $P = 0.0059$; Figure 2.4a). To illustrate the effects of LLD on the probability of relocation, Figure 2.4a shows three different ecological scenarios, based on the results of this relocation analysis. These scenarios illustrate that the effect of LLD on chances of relocation during our field season varied greatly depending on the location of the colony and the week of our study (see Figure 2.4a and its caption for an explanation of the three different scenarios). For a given LLD, the weekly probability of relocation for some colonies could be as low as 0 and as high as 0.15 for other colonies, for example.

The average vapor pressure deficit of the 6 days prior to a census (Average Mobile VPD) was particularly influential, increasing the weekly odds of colony relocation by a factor of 5.7 (570%) for every unit increase (odds ratio = 6.667, $P < 0.0001$; Figure 2.4b). As with the effects of LLD, the effect size on relocation probability depended on several other underlying factors, such as plot location, nest type and week. For example, at the average Mobile VPD during our field season, 1.65 hPa, week to week probability of relocation ranged from approximately 0.1 to as high 0.7.

Effect of Phorid Flies on Chance of Relocation

The mean number of phorids at occupied nest sites was 0.64, and when nests with at least 1 phorid fly present are considered, the mean number of flies was 1.89. The presence of phorid flies at occupied nest sites was relatively low, with only 27.2% of the nest sites having 1 or more flies present. Phorid fly presence was also patchy, as it was common for flies to be present at a colony while being absent at neighboring colonies. The number of phorid flies observed at a bait during a census had no effect on the probability that a colony would relocated the following week (odds ratio = 0.03, P = 0.62).

In summary, relocation chances for a colony was subject to several underlying factors that can either reduce the chances of relocation, such as "tree trunk" nest type or plot "Br 3," or increase the likelihood of relocation, such as "ground" nest type or plot level "Br1 + Br2 + TX1." Additionally, leaf-litter depth and average mobile VPD increased the likelihood of colonies emigrating.

Discussion

To our knowledge, few studies have looked at the biology of relocation behavior of a single ant species in such detail as reported here although see McGlynn et al. (2004). Our research on the relocation of *P. dentata* has revealed a complex story in which many factors play a key role. Colonies relocated frequently, on average every 16 days. We show that many factors influence relocation (Table 2.3). Those nesting by tree trunks were less likely to relocate than if nesting in the soil. High VPD values increased the chances of relocation, and yet, nests under higher leaf litter were more likely to

relocate than those under little leaf litter. This was contrary to the expectation under the hypothesis that high leaf litter helps temper climatic variations. There was no association between phorid fly attacks on foraging columns and the chances of relocating.

Chances of relocation for two different colonies could be dramatically different, depending on the type of nest they inhabited, the plot in which they were located, or the week of study. A group of ants with low probability of relocation were those nesting in plot Br 3 and in tree trunk. Colonies located in any other plot and located in the ground moved most often.

Biology of Nest Relocation

Nest site selection. It was surprising to find that colonies nesting by tree trunks were only 68% as likely to relocate compared to ground dwelling colonies. Unlike the Argentine ant *Linepithema humile,* which locates nest near vegetation (Heller and Gordon 2006), *P. dentata* colonies did not favor areas with herbaceous growth. Tree trunks could rather protect nests against vertebrate predators. In South Africa rocks prevent nest excavation by aardvarks and other vertebrate predators (Dean and Turner 1991). In our habitat, nests with signs of physical disturbance by vertebrates were observed 5 times in our study, and those located by tree buttresses might provide protection against armadillos, which are known ant feeders (Sikes et al. 1990). This might also explain the lower likelihood of relocation of colonies nesting under rocks and inside wood.

Tree trunks might alternatively act as microclimate moderators in the forest environment of our study site, given that air and soil temperatures can frequently exceed 40°C on summer days (submitted). Trees are able to tap water from deep underground aquifers with their roots, allowing them to stay at significant cooler temperatures than the environment (Domec et al. 2006). This could give colonies a cooler and more humid nesting environment.

As in our study, McGlynn and coworkers (McGlynn et al. 2004) found that in days with higher VPD, colonies of *A. araneoides* moved more often. They suggested that when VPD is high there is less chance of rain, so colonies might decide to relocate in these circumstances. *Pogonomyrmx barbatus* (Gordon 1992), *Pheidole desertorum* and *P. hyatti* colonies of southern Arizona (Droual and Topoff 1981b) are more likely to relocate after it has rained, perhaps because nest excavation is easier in wet soil. We did not find any increase of relocation rates after numerous rain events, but colonies might be relocating during drier days to reduce the threat of rain.

The availability of nesting sites in tree-trunks is likely a commodity in short supply, and might explain why the majority of the colonies nested in ground. Alternatively, during the summer, colonies could actually prefer ground nests over the other nest types. Some ants are known to change nest preference throughout the summer. This is hypothesized to be due to colony development. For example, the number of *Aphaenogaster rudis* colonies nesting under rocks and stones decreases, and those nesting in the soil increases, between June and August (Smallwood and Culver 1979a). Seasonal polydomous ants, in which colonies coalesce into one nest in winter and spread to several nests simultaneously in spring and summer, may use this behavior

as a way of thermoregulation (Banschbach et al. 1997) or to collect food resources more efficiently (Buczkowski and Bennett 2008), or both (Heller and Gordon 2006). We did not find any change in nest use throughout our field work, but seasonal preferences for nesting sites of *P. dentata* may occur during other parts of the year.

Competition. Evidence of competition from neighboring colonies as a cause of relocation is scarce. Smallwood (Smallwood 1982a) found no effect of food supplementation on likelihood of relocation of *Aphaenogaster rudis* colonies. In *Pogonomyrmex barbatus*, distance to neighbor has no effect on the chances of relocation (Gordon 1992), and there is no evidence that competition from colonies reduces its chances of survival (Gordon and Kulig 1998). A connection between relocation and competition with neighbors could not be ruled out for the seed-harvesting ant *Messor andrei* (Brown 1999). Competition seems not to play an important role in *A. araneoides* (McGlynn 2004). In a separate study, food supplementation did increase colony density of litter-dwelling species, thus reflecting a possible reduction in exploitative competition among neighboring colonies (McGlynn 2006). In *P. dentata*, the distance of relocation was small ($u \approx 0.76$ m), and baits rarely attracted foragers from more than one colony at a time, suggesting that colonies rarely overlapped in their foraging territory. Because the short relocation distances of *P. dentata* are unlikely to place the colony in areas where it could not forage before moving, relocations are not likely the result of resource depletion. Nevertheless, competition cannot be ruled out as colonies are competing against many species simultaneously.

Phorid flies and relocation. We found no association between phorid fly abundance and relocation. Some ant species do relocate to escape predators or parasites.

Leaf-cutter ants can abandon their nests if they become infected with parasitic fungi (Fernandez-Marin et al. 2003). *P. desertorum* and *P. hyatti* maintain several nests unoccupied as places of evacuation when attacked by army ants (Droual and Topoff 1981a, Droual 1983). McGlynn (2007, 2010) has provided tantalizing evidence showing that *A. araneoides* colonies relocate often to reduce nest odor accumulation, which would allow workers to detect an army ant raid sooner.

In *P. dentata*, reducing the attacks of phorid flies through relocation might not be an efficient use of time or energy. Phorid flies use alarm and recruitment pheromones of ants as cues to identify their hosts (Feener and Brown 1997), and the parasitoids are likely able to detect these pheromones if they are carried by the wind. Because phorid flies can travel relatively fast, phorid presence/absence is likely to change at a much shorter timescale than the 2-week average residence-time of *P. dentata* colonies. In addition, the average relocation distance of 0.76 m is not likely to alter the likelihood of phorid flies finding a colony which has moved. Although reducing exposure to phorid flies should be greatly beneficial to colonies, it appears that they have not been able to escape from these parasitoids through relocation.

Leaf Litter depth and habitat complexity. P. dentata colonies preferred nest sites with lower leaf litter depth. Species such as *P. dentata*, which are mass recruiters, might prefer less complex habitats to be able to quickly reach and dominate food resources (Lassau and Hochuli 2004). Complex habitats may limit the advantage of recruiting large numbers of foragers and soldiers before other competitive species arrive first. Nevertheless, Wilkinson and Feener (2007) found that *Pheidole diversipilosa* and *P. bicarinata* can actually benefit from higher habitat complexity because soldiers could

use the leaf-litter as refuge against attacks by phorid flies. Leaf litter could actually produce both effects on ants, and, for *P. dentata*, leaf litter depth preference might depend on whether colonies are subject to high number of phorid fly attacks. In the case of high number of attacks, they might prefer higher complexity. Alternatively, rapid domination of food resources may be more important than parasitoids. We do know that *P. dentata* soldiers use leaf-litter as refuge, so further experimentation is needed to determine whether colonies experience a trade-off between better protection against parasitoid flies or better foraging efficiency.

Economy of Nest Relocation

Our view of nest relocation has evolved as we learn more about who relocates and how often. Ants were considered to be in all respects sessile organisms, forced to relocate only in response to catastrophic events (Wilson 1971, Smallwood 1982b). We now know that this behavior is widespread and likely follows a continuum, from species that emigrate occasionally, such as *Atta colombica* (Rockwood 1973) and *Pogonomyrmex* species (Carlson and Gentry 1973, Gordon 1992), to species that relocate several times each month or week (Smallwood 1982a, Maschwitz and Schönegge 1983, Tsuji 1988, Freitas 1995). Relocation behavior is common in many phylogenetically distant species (McGlynn 2012) and follows stereotyped and elaborate behaviors (Möglich 1978). Relocation in ants appears to be a natural part of the life of many species of ants.

Relocation, though, needs to be reconciled with the fact that moving colonies is not cost free. Colonies heavily invest in constructing new nest sites (e.g., Tschinkel

2003). Exposing the queen to potential predators on her way to her new home also has risks. Costs associated with relocation are likely to increase with larger colony sizes (Smallwood 1982b). Larger colonies, such as *Atta cephalotes* (McGlynn 2012) and *A. colombica* (Rockwood 1973), are less likely to relocate than litter dwelling ants, such as *Tapinoma sessile* (Smallwood 1979), or the numerous twig dwelling ants of a rainforest floor (Byrne 1994).

Our data on *P. dentata's* frequent relocations might shed light on the cost/benefit conundrum. How can we interpret *P. dentata's* frequent relocations? One scenario is that relocation in *P. dentata* is costly, and occurs only when there is the risk of the death of the colony. In this case the relocation is forced (see Wilson 1971). From this perspective, moving is performed only when no better alternative is available (e.g., escaping an army ant raid is preferable to trying to defend the nest from the invaders). For *P. dentata*, this "high disturbance" interpretation is difficult to support from an ecological perspective because it would imply a high frequency of "catastrophic" events per colony per month. Although we did observe some nest sites disturbed by animals, likely armadillos, these cases were rare, and we found no evidence that other disturbance events happen frequently enough to explain these high relocation rates. Also, *P. dentata's* ecological success, through its ability to dominate food resources and its abundance in the forest floor (Wiescher et al. 2011), would be difficult to understand if colonies were under constant stress.

A more likely interpretation is that, for *P. dentata*, the costs of relocation are not high. Circumstantial evidence indicates that this species keeps costs low: colonies appear to invest little in constructing new homes. Several nests that we excavated

revealed that ants nested in cavities of the leaf litter, and if there was excavation, it was minimal (unpublished data). Additionally, colonies might reduce the cost of relocation by moving quickly. Both moves we observed last about 20 minutes. Our data agree then with the general trend of low cost of relocation observed in other species with small colony sizes.

In addition to the costs, relocation should be examined in the context of the total energy balance of a colony's economy. Given that costs are likely small for our study species, the colonial / ecological advantages obtained from relocation could be relatively small, but still worthwhile for the colony if they were greater than the costs. In this scenario, the energy budget would tip the balance in favor of frequent relocations. Future work should address the benefits of relocation in *P. dentata*.

With this study we have attempted to identify the key environmental factors that affect the probability of relocation in *P. dentata*. Our study has shown that the underlying factors affecting relocation in *P. dentata* are numerous, and that they act simultaneously on colonies. It is also possible that other factors we did not measure, such as circadian rhythms, temperature and humidity conditions inside the nest, and health condition of the colony and the nest, affect relocation. More research is needed to determine the cost and benefits of relocation, both in *P. dentata* and in other species, so that ultimately we might have an understanding of the geographic, ecological or phylogenetic correlates to this interesting behavior.

Acknowledgments

We are particularly grateful to Anthony Ho for his invaluable help during field work. We want to thank Larry Gilbert at the University of Texas in Austin, John Crutchfield at Brackenridge Field Laboratory (BFL)**,** and the rest of the staff at BFL for kindly providing access to the field station, lab space, and weather data. Richard McElreath and Fred Adler provided instrumental help with the statistics. Philip Wiescher shared valuable thoughts and ideas. Funding was provided by the University of Utah, a National Science Foundation GK-12 Fellowship to M. M., and National Science Foundation grants DEB-0316524, DGE-0841233 and 10510-52352 to D.H.F.

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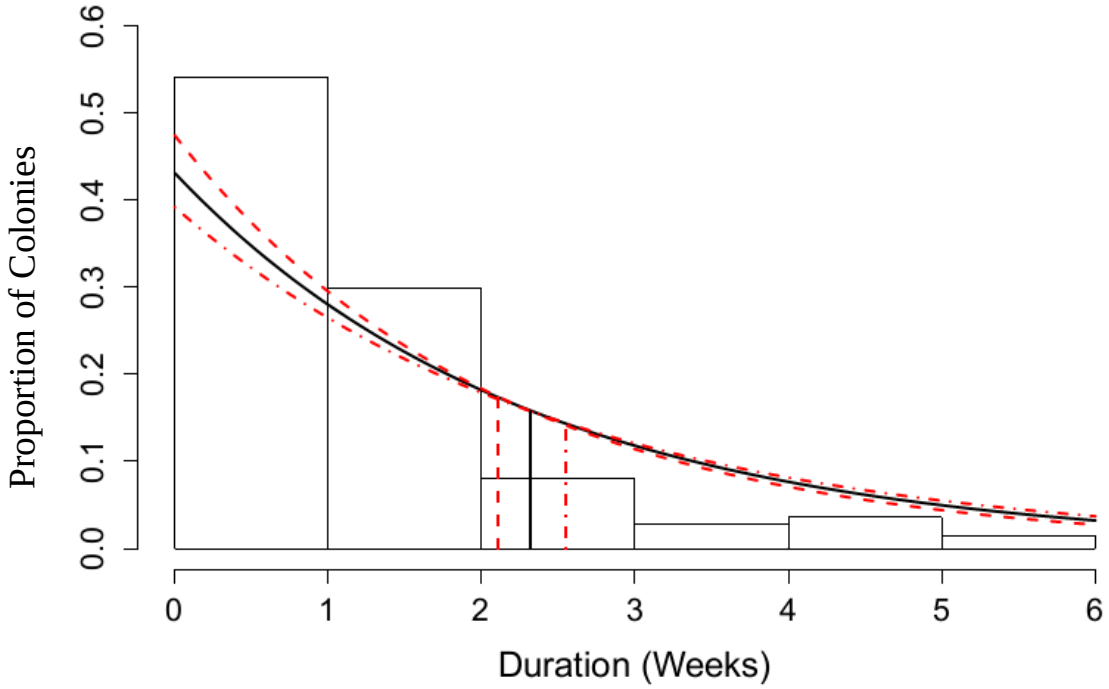

Figure 2.1. Histogram of nest duration in weeks (*n* = 517). Curves represent the following: negative exponential estimate (solid line), lower 95% CI (dotdashed line) and the upper 95% CI (dashed line). Vertical solid line shows the mean survival time (2.31 weeks or 16.2 days); dashed vertical line the lower 95% CI (2.11 weeks or 14.75 days); dotdashed vertical line the higher 95% CI (2.54 weeks or 17.85 days).

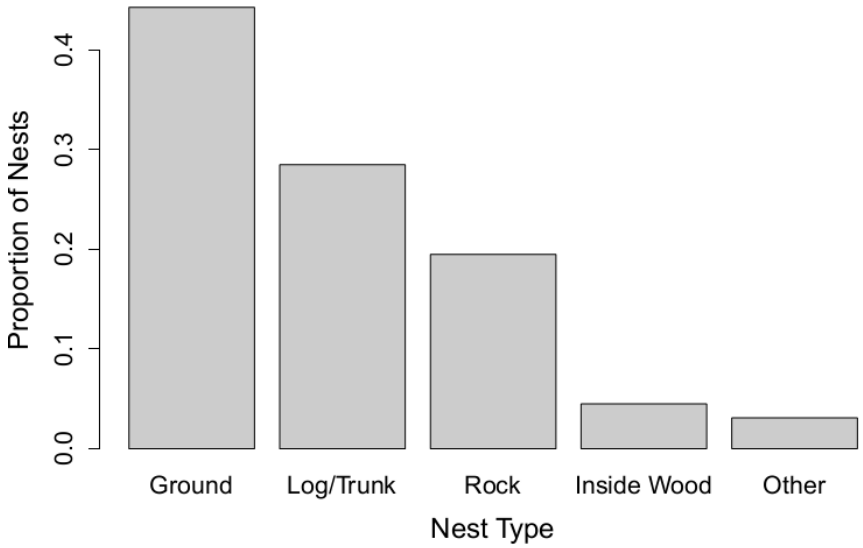

Figure 2.2 Proportion of *P. dentata* nest types in BFL (*n* = 445)

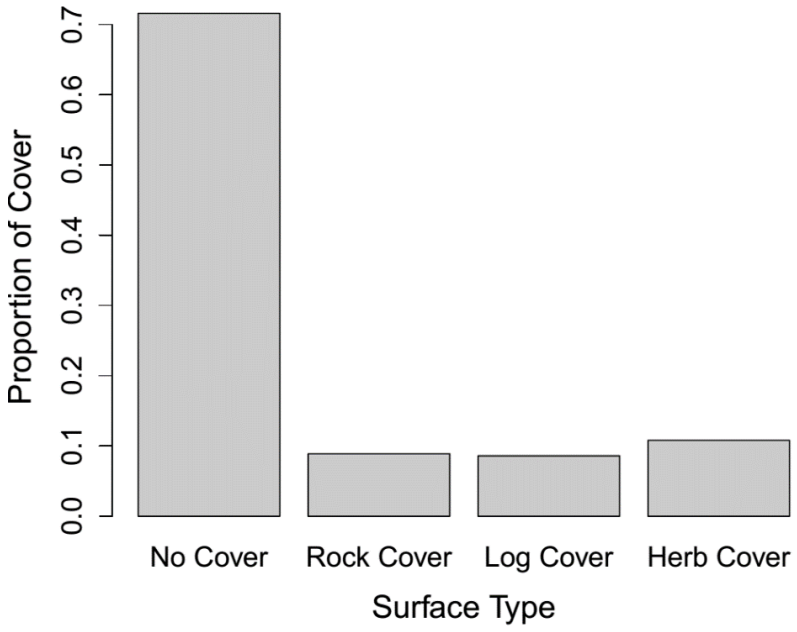

Figure 2.3. Proportion of cover at nest sites of *P. dentata* by low lying herbaceous plants, rocks and decaying wood (*n* = 445)

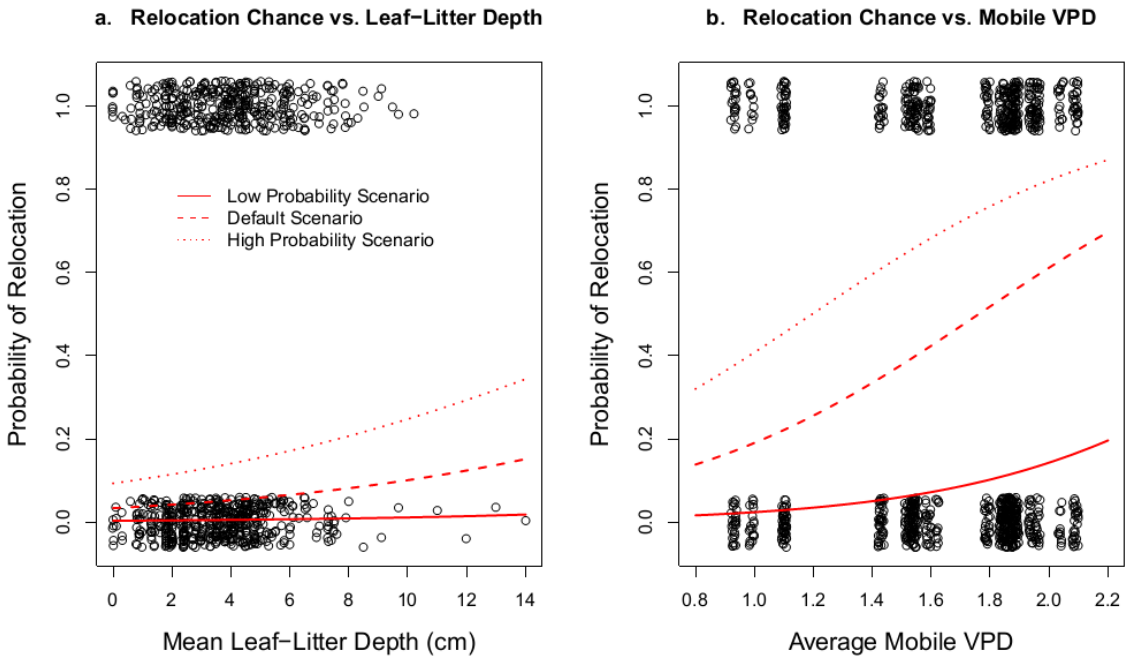

Figure 2.4. Relationship between probability of relocation and mean leaf-litter depth in **a** and average mobile VPD in **b**. In each graph, the estimated probabilities of relocation under three different scenarios are shown. "Low Probability Scenario" (solid lines) corresponds to colonies in plot Br 3 and week 4 and tree trunk nest, factor levels which reduced the odds of relocation. "Default Scenario" (dashed lines) corresponds to factor levels selected as intercept (Plot: Br1 + Br2 + TX1; Week: 1 + 2 + 3; Nest Type: "ground"). "High Probability Scenario" (dotted lines) corresponds to factor levels which increased the odds of relocation (Plot: Br1 + Br2 + TX1; Week: 5; Nest Type: "ground"). Observe that the effect of mobile VPD on probability of relocation is much stronger than the effect of leaf-litter depth, although both covariates, with increasing amounts, increase the chances of relocation. Artificial jitter has been added to the data points to make them more visible

Table 2.1. Covariates used in the 3 analyses carried out in this paper. Abbreviations of the analyses are: NR - probability of nest relocation. PHO - phorid fly analysis. SUR - survival analysis

Covariate		Data Type	Levels/Units of Measurement	Analysis
Plot		Categorical	Br 1; Br2; Br 3; Br 4; TX1; TX3	NR
Week		Categorical	Week 1 to 6	NR
Ground Cover		Continuous	from 0% to 100%	NR
Leaf Litter Depth		Continuous	cm (0 truncated)	NR
Nest Type		Categorical	"ground"; "rock"; "tree trunk"; "log"; "other"	NR
Infrared Surface Temperature of Nest		Continuous	°C	NR
Infrared Surface Temperature of Ground		Continuous	°C	NR
Air Data	Maximum Temperature	Continuous	°C	NR
	Maximum Relative Humidity	Continuous	°C	NR
	Maximum VPD	Continuous	kPa	NR
	Minimum Temperature	Continuous	°C	NR
	Minimum Relative Humidity	Continuous	°C	NR
	Minimum VPD	Continuous	kPa	NR
	Average Temperature	Continuous	°C	NR
	Average Relative Humidity	Continuous	°C	NR
	Average VPD	Continuous	kPa	NR
7-Day Rain		Continuous	mm	NR
Phorid Fly Density		Count	0 truncated	PHO
Time to Moving		Count	day	SUR

Table 2.2. Analysis of variance table showing the effects of nest type and plots on leaf litter depth.

	df	Sum Sq	Mean Sq	*F* value	*P* value
Nest Type	4	34.1	8.5	2.6	0.0364
Plot	5	151.9	30.3	9.2	<0.0001
Nest Type x Plot	17	89.9	5.2	1.6	0.0595
Residuals	418	1376.6	3.2		

Table 2.3. Coefficient estimates for the best fit glmmML model, based on AIC. The table shows the treatment contrasts with their respective proportional change in odds (PCO). PCOs lower than 1 reduce the chances of nest relocation, and PCO with value higher than 1 increase the chances of relocation with respect to the intercept.

Factor	Coefficient	Std. Error	*z* value	*P* value	Proportional Change in Odds
1. Intercept	-3.3425	0.846	-3.951	<0.001	0.035
2. Plot Br 3	-0.9047	0.238	-3.797	<0.001	0.405
3. Plots Br4 + TX1	-0.4776	0.181	-2.639	0.008	0.620
4. Week 3	-0.5213	0.224	-2.331	0.020	0.594
5. Week 4	-0.9485	0.238	-3.978	<0.001	0.387
6. Week 5	1.0737	0.379	2.837	0.005	2.926
7. Tree Trunk Nest Type	-0.3878	0.185	-2.100	0.036	0.679
8. Rock + Inside Wood Nest Type	-0.1964	0.201	-0.979	0.328	0.822
9. Other Nest Type	-0.7599	0.505	-1.503	0.133	0.468
10. Mean Leaf-Litter Depth	0.1160	0.042	2.751	0.006	1.123
11. Mobile VPD	1.8987	0.483	3.935	<0.001	6.677

CHAPTER 3

NEST RELOCATION OF THE ANT *PHEIDOLE DENTATA* (HYMENOPTERA: FORMICIDAE) AS A THERMOREGULATORY BEHAVIOR

Abstract

Social insects have sophisticated nesting behaviors, which are paralleled by various thermoregulatory strategies that allow colony members to remain within narrow temperature limits inside nests. Given the lack of wings in ants, their methods for controlling nests temperature (T) are more limited than in bees and wasps. Nest relocation in ants has been proposed as a form of thermoregulation, although this hypothesis has seldom been studied.

We investigated thermoregulation in *Pheidole dentata* in a humid, subtropical habitat. We recorded nest type, leaf litter depth, and paired temperatures in the nest and surrounding soil. We paired 1) internal nest T with underground soil T, and 2) nest surface T and soil surface T. Air temperature was also measured throughout the study period. Internal nest temperatures (INT) varied less, and were 2.4°C cooler than the average air temperature; INT was also less variable than underground soil temperatures. There was no effect of nest type on INTs, yet leaf litter depth significantly reduced

INTs. Nest surface temperatures and internal temperatures warmed up significantly less than the corresponding soil surface and underground temperatures. In addition, colonies appear to avoid nesting in locations which reach surface temperatures greater than 38°C.

Colonies are clearly selecting cooler locations than their surroundings, and this leads to lower average internal and surface temperatures than the paired spots. Colonies might have important physiological and ecological reasons to limit high temperatures, the later related to *P. dentata* being a mass recruiter. Further implications of this behavior are discussed.

Introduction

Social insects are unique in the animal world for their sophisticated nesting behaviors. Although animals commonly use a variety of crevices, tunnels, and burrows as places for hiding, nesting and reproduction, social insects represent the prime example of natural architecture. Their nesting habits and structures are the most diverse and developed (Wilson 1971). For a staggering diversity of biomes and ecosystems, nests provide a protected space to species of different colonial sizes and feeding specializations.

Social insects require narrow ranges of temperature for normal development (Jones and Oldroyd 2006). Hence the complexity and diversity of nests likely arose as adaptations that increased the thermoregulatory control of the nest on the part of the workers. Additionally, in response to the needs of the colony and ambient conditions,

ants have various mechanisms to effectively reduce or increase nest temperatures (Jones and Oldroyd 2006).

To increase brood temperature, most species of bees and wasps can use metabolic heat. For example, the honey bee (*Apis mellifera*) can maintain the brood between 28°C and 32°C even when ambient temperature is 10°C (Kronenberg and Heller 1982). Some ant and termite species with large colony sizes can also take advantage of metabolic heat. For instance, the wood ant *Formica polyctena* of central Europe is able to maintain constant nest temperatures, throughout its active period, using the heat of workers and the organic decomposition inside the nest (Frouz 2000). Bees and wasps can actively cool warm nests when workers "fan" or circulate air in the nest by flapping their wings (Ishay et al. 1983, Vogt 1986, Hölldobler and Wilson 1990). Should fanning be insufficient, bees and wasps also resort to evaporative cooling, whereby workers bring water into the nest to lower temperature through evaporation.

Even though ants occur in a staggering number of diverse ecosystems and climates (Hölldobler and Wilson 1990), their thermoregulatory repertoire is more limited than that of bees and wasps. The lack of wings in workers precludes colonies from fanning their nests (Jones and Oldroyd 2006). Additionally, the use of metabolic heat is limited to large colonies composed of thousands or millions of workers, as is the case of the army ant *Eciton burchelli* (Franks 1989) and *Formica* spp. wood ants (Frouz 2000). In temperate areas 80% of species have small colonies of 10 and 1000 workers (Kaspari and Vargo 1995), and many species nest in small cavities and in leaf litter (Smallwood 1982, Herbers 1989), reducing opportunities for control of temperature.

Small colonies are less able to control nest conditions than species with bigger ones (Möglich 1978), and it has been suggested that colonies might relocate their nest to a new location as a form of thermoregulation (Smallwood 1982, McGlynn et al. 2010, Soare et al. 2011), just as many reptiles thermoregulate behaviorally by moving to the appropriate environmental temperature.

The thermoregulatory challenges faced by colonies will depend on regional and local factors, such as geographical location (Kaspari and Vargo 1995), season of the year, and the local microhabitat of the nesting site. In temperate and subtropical regions, summer is the season to produce workers and reproductive. Hence, this is likely to be the most critical and difficult season, since the colony must acquire food in a competitive environment under potentially stressful ambient conditions (Cerdá et al. 1997). Also, the external environment can profoundly affect the temperature and humidity inside nests (MacKay 1981, Fernández Escudero et al. 1993, Frouz 2000, Robinson 2008), especially if located in shallow areas such as in the leaf-litter, twigs, or under rocks. In these circumstances, the type of nest and its location acquire a definite importance. These factors will not only shape access to resources and the competitive landscape, they will also determine the microenvironment inside the nest and the environment encountered by foragers outside the nest.

Few studies have addressed the use of nest relocation as a form of temperature control or quantified how nests differ thermally from the soil in general. In a previous study (Chapter 2), we showed that colonies of *Pheidole dentata*, an abundant species of the southeastern United States, nest on a variety of locations, mainly in the soil, by tree trunks, and under rocks and rotting wood. In addition, they relocate their nest sites

frequently, on average once every 16 days, and we showed that numerous factors, such as nest type and leaf litter depth, either increased or decreased chances of relocation. Nevertheless, the use of relocation as a possible form of nest thermoregulation was not addressed. Air and ground surface temperatures can frequently exceed 40°C in woodland habitats of central Texas. This represents a thermal challenge to many ant species, including *P. dentata*. We hypothesize that colonies choose nest sites that are cooler than surrounding areas, and are quick to change nest sites to accomplish this goal. Here, we report that *P. dentata* nests warm at a lower rate compared to the environment at large, consistent with a thermoregulatory behavior.

Materials and Methods

Study Site

This research was carried out at Brackenridge Field Laboratory (BFL), located in Austin, Texas, as part of a study on nest relocation of *Pheidole dentata*. Data were collected from May to July of 2008 concomitantly with gathering of relocation data. BFL, a 33 ha reserve located on the Colorado River, contains abundant natural vegetation consisting of live oak – ash juniper forest (McMahan et al. 1984) and natural meadows. The climate is humid subtropical, with warm humid summers and cool winters; rain occurs throughout the year, although the wettest months are May and June (with 110 mm and 109 mm of rain, respectively), and the driest month is July (National Climatic Data Center 2012). Temperatures in summer are hot, with an average maximum of 32°C and 35°C between May and August, yet the summer of 2008 was

hotter and drier than average in the Travis County area (Nielsen-Gammon and Adian 2008).

A large proportion of soils at BFL are of the Tarrant series, which consist of shallow, well-drained, stony and clayey soils overlying a limestone bedrock (National Cooperative Soil Survey 1974). At our study site *P. dentata* ground nests were often shallow, found within the first 15 cm of soil, although they can occasionally be up to 30 cm deep (M. Moyano, pers. obs.). Nest sites were covered by an average of 5 cm of leaf litter (range 0-14 cm) (Chapter 2).

Experimental Design

Six 50 m x 50 m plots were selected in forest habitat; plots were at least 50 m from each other. At four randomly chosen plots HOBO Data loggers were set up to record air temperature and relative humidity every 5 minutes for the duration of our research.

We found occupied nests by placing pecan cookies on plastic cards every 10 m and following workers carrying crumbs back to their nests. We marked nests with survey flags and each colony was assigned a unique code which allowed us to track colonies as they relocated to new nest sites. In each plot roughly 30 *P. dentata* nests were initially marked, although this number increased as new colonies were discovered throughout our study. In total, 540 nest sites were studied, which belonged to 220 colonies.

We performed a weekly census on each plot with the objective of understanding the relocation behavior of colonies; these data are presented in Chapter 2 and further

information on the census methods can be found there. During each census we also gathered temperature data, which is presented here. We classified nests into five different nest types: 1) “ground” nesting colonies nested in the soil or leaf litter; 2) “tree trunk” colonies nested between the soil and the roots of trees; 3) “rock” colonies nested in rock cracks or underneath rocks; 4) “inside wood” colonies were found inside twigs or fallen branches in the ground; and 5) “other” for colonies dwelling in any other nesting situation, such as inside bricks, or buried glass bottles.

Leaf litter depth was measured using a 50 cm x 50 cm quadrat placed over the nest site; the quadrat was divided into four equal-sized areas of 25 cm x 25 cm with strings. Four measurements were done in each quadrat and the average used for analysis.

Methods of Temperature Recordings of Nests and Air

Nest recordings. Temperature was measured from nests using two different methods. First, internal nest temperatures (INT) were recorded using two Hobo Micro Station data loggers (Onset Computer Corporation, Bourne, MA, USA), each one provided with two temperature probes that could record data independently. Two nests had internal temperatures monitored at any one time throughout the study period. Underground temperature recordings were paired: one probe was inserted inside the nest (INT) and the second probe was inserted into the ground (underground soil temperature or UST) as control, in a randomly chosen location 1 m away from the nest. Control and nest temperature probes were inserted 5 cm into the soil given that rocks often restricted placing the probes deeper. Prior to inserting the probes we removed a

small area of leaf litter so as to count 5 cm from the top of the soil; we later replaced the leaf litter to resemble its original depth. In total we collected temperature data on 15 nest-control pairs (nest plus soil paired measurements), each recording lasting between 4 and 7 days.

Second, external (surface) nest temperatures were recorded at every active nest on a weekly basis during each census. Using infrared thermometers (Meterman IR608), paired measurements were obtained at each active nest site: one surface measurement was obtained at the nest opening (nest infrared) and subsequently a second control reading was obtained at a randomly chosen spot 1 m away from the nest opening, where no nest was present (soil infrared). Different pairs of measurements were collected during various times of the day and throughout the study season. Given that we were primarily interested in the temperature difference between nest and ground temperature, the paired measurements allowed us to control for different time periods.

Air recordings. Air temperature was measured at BFL with 4 Hobo H8 Pro Series loggers (Onset Computer Corporation., Bourne, MA, USA), which were set to record temperature every 10 minutes. The loggers were placed at the center of each of four randomly chosen plots and their data was later averaged into a single dataset. This dataset was used for all our analyses. All six data points from each hour were averaged into 1-hour values, so for each day 24 1-hour values of temperature were obtained.

Study of Thermoregulatory Behavior

Effect of leaf-litter on internal nest temperature. We investigated the effect of leaf litter depth (LLD) on internal nest temperatures by correlating it with internal nest

temperatures. Given that greater leaf-litter depth increases the chance of a colony relocating to a new nest site (Chapter 2), we measured leaf litter depth over nest sites to understand its overall effect on internal nest temperature. A single temperature value for each nest was obtained by averaging the internal temperature data. Since our analyses showed that nest type did not have any effect on internal temperature of nests (see Figure 2.3), we compared all nest types with leaf litter in the analysis.

Analyses of paired temperature measurements. The forest ground warms up mainly (but not exclusively), by two routes: through direct exposure to sunlight, and indirectly by the sun's energy being re-emitted as infrared radiation by the surrounding air and objects. The forest floor is likely to be a mosaic of different temperatures due to the uneven shade provided by the canopy, giving colonies a chance to select among nesting sites of different temperature qualities. We expect colonies to avoid warmer locations in favor of cooler sites, given that soil temperatures can commonly exceed 40°C (preliminary data). If colonies are indeed thermoregulating through relocation, we would then observe 1) nest surfaces to have, on average, cooler temperatures than comparable surfaces without a nest, and 2) underground nest temperatures to be (on average) lower than comparable underground soil temperatures with no nest.

Our data allowed us to do the following analyses based on paired measurements: First, regress nest surface temperature vs. ground surface temperature. Second, regress nest internal temperature vs. soil underground temperature. Third, ANCOVA comparing the slopes of nest and soil surface temperatures vs. air temperature, to determine if nest surfaces and soil surfaces warm equally given a certain air temperature. We analyzed surface and underground paired temperature datasets using

linear regression to model the slope of each data set. These analyses test whether nest temperatures warm up more, less or equal than the corresponding surface or underground temperatures (a slope less than 1 would mean that nest sites warm less than the environment, while a slope greater than 1 would show that nests warm more than the environment). 4) We analyzed whether daily maximum and minimum temperatures of the air correlate with daily maximum and minimum internal temperatures of nests. Given that internal nest temperatures (INTs) were measured in two nests simultaneously, we obtained maximum and minimum INT for each nest for each day, and averaged these values to obtain one maximum INT and one minimum INT per day. These values were correlated with MaxAT and MinAT for the analysis.

Effect of nest type on internal temperatures. We tested whether nest types had significantly different internal nest temperatures (INT) using an ANOVA. Given that INT recordings of different nest types were gathered throughout 6 weeks, direct comparison was not possible as nest temperatures could have varied with external conditions, such as air temperature, cloud cover or rain, in addition to possible effects of nest type itself. To correct for this time component, we used the temperature difference between the nest (internal) and the air as our dependent variable. These data were obtained the following way: each 1-hour INT value was subtracted from the 1-hour air temperature value corresponding to the same day and hour; a positive value meant that the air was warmer than the nest, and a negative value corresponded to the air being cooler than the nest.

Statistical Analyses

All statistical analyses were completed in R 2.13 (R Core Team 2012). To study the relationship between surface heating of nest vs. surface ground heating, we ran several theoretical linear models against the data. The best model was selected with Akaike's Information Criteria (AIC), which chooses models based on the log-likelihood and the number of explanatory variables of each model.

Results

Temperatures inside *P. dentata* nests at 5 cm below ground level were more stable and fluctuated considerably less than ambient air temperature, and, on average, internal nest temperatures were 2.4°C cooler than the air (26.60°C ± 1.45°C for nest vs. average air temperature of 29.04°C ± 4.56°C (mean ± SE, $P < 0.0001$, $F_{(1, 1326)} = 1997$); Figure 3.1a). The comparison between internal nest vs. underground soil temperatures reveals that nests were 0.7°C cooler than the soil (means of 26.56°C and 27.27°C, respectively; $P < 0.0001$, $F_{(1, 5354)} = 244.5$), and nest temperatures were significantly less variable than soil temperatures (ratio of soil/nest variances = 1.57 (CI 1.46 - 1.70), $F_{(2677, 2677)} = 1.57$, $P < 2.2 \times 10^{-16}$, Figure 3.1b).

Given that nests were protected from external conditions, temperatures rarely reached the extreme high temperatures that were common during the hot Texas summer, and also remained warmer at night than the air (Figure 3.1b). The mean daily maximum air temperature (MaxAT) and mean daily minimum air temperature (MinAT) were 35.98°C and 23.64°C, respectively. The average time of MaxAT and MinAT during our field season happened at 3:16 pm and 6:18 am, respectively. The average

daily maximum and minimum underground temperatures of nests at 5 cm depth were 28.28°C and 25.27°C, respectively (N = 16). Nests reached their maximum temperatures on average 30 minutes after MaxAT, and their lowest temperature approximately 55 minutes after air temperatures fell to MinAT.

Although nest temperatures rarely approached the extremes of ambient temperatures, there was a positive regression between daily maximum and minimum temperatures inside nests and those of the air. MinAT significantly regressed with minimum INT (t = 5.01, $d.f.$ = 46, P < 0.0001, r^2 = 0.29; Figure 3.2a); likewise, MaxAT significantly increased with maximum INT (t = 7.02, $d.f.$ = 45, P < 0.0001, r^2 = 0.52; Figure 3.2b), although their slopes were different: nest temperatures responded more rapidly to high maximums than low minimums (slopes 0.63 vs. 0.25, respectively).

Also, daily internal minimum temperatures significantly regressed with daily internal maximum temperatures for each nest, i.e., a relatively warm nest during the day would be a relatively warm nest at night (linear model: Minimum INT = 0.4 * maximum INT + 14.08, P = 0.024), with maximum INT explaining 38% of the variation of minimum INT.

P. dentata colonies nested in a variety of nest types: most colonies nested in the soil (44.3%), by tree trunks or under fallen logs (28.5%), underneath stones (19.5%), or in rotting logs (7.5 %), (see more details in Chapter 2). Underground nest temperatures did not differ significantly by nest type (Table 3.1; due to limited sample size, comparison was done between ground, tree trunk and rock nest types; Figure 3.3). On the other hand, internal nests temperatures did vary with LLD (Figure 3.4). There was a significant negative regression between LLD and internal nest temperatures (*slope* = −

0.32, *intercept* = 27.47, $F_{(1, 14)}$ = 6.47, P = 0.0234), with LLD explaining 32% of the variation in nest temperature.

Nest Thermoregulation

The relationship of ambient air temperature vs. nest and soil surface temperatures. In the analysis of covariance, surface temperature source (nest or soil) vs. air temperature interaction was not significant. Thus, both nests and soil warmed the same amount with respect to a particular air temperature (slopes 0.92, $F_{(1, 1750)}$ = 2494.5, $P < 2.2 \times 10^{-16}$; the P value is for the air temperature variable in the model without the interaction; Figure 3.5). Nests had a lower intercept, as nest surfaces were on average 0.49 °C cooler than the forest soil surfaces in general ($F_{(1, 1750)}$ = 17.74, $P < 2.66 \times 10^{-5}$). On average, the soil and nests remained cooler than the air during daylight, although nests were on average cooler than the forest floor.

Paired infrared temperature measurements. Nest surfaces heat up less compared to the paired ground surfaces. The model that best explains the data, based on AIC, is the 3rd order polynomial regression (Table 3.2; Figure 3.6). At low to moderate temperatures, the preferred regression line is practically indistinguishable from the expected line, which, with its slope of 1, indicates that a unit increase of ground surface temperature is accompanied by a unit increase in nest surface temperature. These models begin to diverge at approximately 35°C as the preferred model curves downward. Although the remaining models disagree in the position of the best fit line at low temperatures, all the models agree with the preferred model by falling below the expected regression line at higher temperatures. These models, especially the 3rd order

polynomial and the quadratic regressions, interestingly suggest that colonies avoid nesting in places where surface temperatures can heat up above 38°C.

Paired underground temperature measurements. Underground temperatures of nesting sites warmed significantly less than surrounding underground areas; on average, for every degree increase in soil temperature there was a 0.59 degree increase at the nest site ($F_{(1, 14)}$ = 16.62, P = 0.0011, Figure 3.7a). Figure 3.7b shows that as underground soil temperature (UST) increases, the difference between INT and UST increases significantly (*slope* = -0.41, $F_{(1, 20)}$ = 11.67, P = 0.0027), as nests warm-up to a lesser degree than the soil. Both paired measurement analyses suggest regulatory behavior by colonies, as they were able to select nest sites that remained cooler on the surface than the environment at large. This effect translated into a cooler environment inside the nest that was on average 0.7°C cooler than adjacent sites.

Discussion

In this study we provide evidence that nest site selection in *Pheidole dentata* is a thermoregulatory behavior and likely plays a key ecological role in the life of this species. *P. dentata* colonies preferred cooler nesting sites than their surrounding environment, as the internal and surface temperatures of nests were cooler than the internal and surface temperatures of the soil (Figure 3.1). Their nests were not only cooler than the average air and soil temperatures, but the temperature difference between nest sites vs. their surrounding environment increased as the air and soil surface temperatures increased (Figure 3.7b).

The soil at *P. dentata* colonies acted as a temperature buffer, as temperatures inside nests varied less and were lower compared to temperature of the air. Ants commonly nest underneath rocks and logs because of their ability to heat-up rapidly in the morning and because they remain warmer at night after the soil has cooled (Fernández Escudero et al. 1993, Robinson 2008). In addition, colonies are apparently choosing to nest by rocks or wood buried in the soil which could provide additional temperature stability, as internal temperatures of nests were significantly less variable than underground soil temperatures at 5 cm (Figure 3.1a).

Although the effect of leaf-litter depth on internal nest temperatures was highly variable (Figure 3.4), its net effect was to reduce temperature at nests. The effect of leaf litter on soil temperature is likely greatest when under the sun as compared to when it is in the shade (Sydes and Grime 1981, Molofsky and Augspurger 1992), which could explain the high variability of litter on nest temperature. Despite the protection from extreme temperature provided by the leaf litter and the soil, nests were not immune to ambient temperature, as the maximum and minimum temperatures of nests and the air were correlated.

It was previously shown that leaf litter depth increases the likelihood of colonies relocating to a new nest site (Chapter 2). In light of our current findings, the effect of LLD on relocation chances are peculiar, because they suggest that colonies would benefit from a deep layer of LLD to maintain cooler nest temperatures. This paradox can be explained if leaf litter is also disadvantageous to colonies, such as making the surrounding habitat more complex and less desirable to *P. dentata* ants (Lassau and Hochuli 2004, Gibb and Parr 2010), and indeed there is evidence that *P. dentata* ants

select habitats based, at least partly, due to leaf litter (Wiescher et al. 2012). If this is the case, *P. dentata* colonies might be faced with a trade-off between seeking protection against heat and foraging in locations of low complexity.

Nest Site Selection

Species differ in their preference to nest in warmer or cooler sites, and their preference is likely to depend on various factors, such as the type of habitat, latitude, season, or the species itself. Although the data available in the literature are scarce, a latitudinal trend is indicated. For example, in places with short summers, such as high latitude boreal forests, carpenter ants prefer to maximize heat intake from the environment by nesting in sunny, open patches of the forest (Chen et al. 2002) and *Formica* spp. use metabolic heat from workers and microbes to warm their nests above the ambient temperature (Coenen-Stass et al. 1980, Frouz 2000). In temperate forests, with their cold winters and warm summers, temperature preferences appear to be seasonal, with ants preferring warmer places in the colder times of the year and cooler places in summer or early fall when temperatures near the surface are hotter (Smallwood and Culver 1979, Tsuji 1988, Gibb and Hochuli 2003). In the tropics, *Ectatomma ruidum* prefers to nest in cooler areas (McGlynn et al. 2010) and the army ant *Eciton burchellii* changes bivouac site mostly at night, presumably to reduce stress from heat (O'Donnell et al. 2009). Although our study cannot say if temperature preference of *P. dentata* is seasonal, its behavior agrees with this general latitudinal trend in which colonies select sites that remain cooler than the soil. Additionally, nests were never found in open, grassy areas, which were generally dominated by

thermophilic species, such as *Pheidole bicarnata*, *Monomorium minimum* and *Solenopsis invicta.*

Thermoregulatory repertoire in ants is likely to depend on colony size, as larger colonies will be able to dig deeper nests. It is known that nest depth in ants is a function of colony size (Buhl et al. 2005), and nest depth can range from the surface of leaf litter in twig-dwelling species (Smallwood and Culver 1979, Byrne 1994) to several meters below the surface (Hölldobler and Wilson 1990, Tschinkel 2003). A species with large colonies, which dig through a greater profile of the soil, will have a larger temperature gradient throughout the nest than species with small colonies (all else being equal). For example, colonies of the red imported fire ant, which can be up to two m deep (Tschinkel 2003) are known to relocate the brood inside the nest throughout the day (Seeley and Heinrich 1981, Penick and Tschinkel 2008). In the neotropical leaf-cutting ant genus *Acromyrmex*, Bollazzi et al. (2008) found that colonies build shallower nests in the cooler thermic soils, compared to those colonies that nest in warmer climates with hyperthermic soils, which nest at deeper levels where the soil is cooler.

In the case of species with small colonies, internal temperatures could potentially surpass optimum or critical values for brood development or colony growth given that nests are likely to remain shallow (Banschbach et al. 1997, Bollazzi et al. 2008). Also, smaller temperature gradients inside the nest would make internal nest migrations less useful. Instead, colonies might need to relocate to new locations that have the optimum microclimatic conditions that the colony requires, and smaller colonies are likely easier to move.

There is abundant evidence that ant workers are able to use a variety of cues during house hunting that inform them of the quality of potential nesting sites (Dornhaus et al. 2004, Franks et al. 2007, Cao and Dornhaus 2012), such as chamber size, distance to food, presence/absence of dead nest mates, etc. Ants are also very sensitive to soil temperatures and will stop digging a nest if the temperature is not the preferred one (Bollazzi et al. 2008). Our results support these findings, as *P. dentata* nest had cooler surfaces than the rest of the soil (Figure 3.6a), cooler underground temperatures and less temperature variations than surrounding soil (Figure 3.1a). And even though the average internal temperature of nests was only 0.71°C lower than average underground soil temperatures, the difference between nest and soil temperatures increased with increasing soil temperatures (Figure 3.7b). Nevertheless, under stressful conditions, a small colony will more likely need a new nest site than a larger colony.

Given that soil temperature greatly depends on the amount of sunlight that it receives (Morecroft et al. 1998), during the hot seasons, colonies should be motivated to search for shaded areas for their nesting sites. Our data suggests that *P. dentata* in fact avoided sunny locations in the forest. If we compare the degree of warming of the soil surface with respect to air temperature, the temperature increase was the same for nest surfaces as for soil surfaces (Figure 3.5), which suggests that nests and nonnests surfaces behaved in similar ways to warming by air. Thus, (if we ignore differences in heat capacity) any surface temperature difference between nest and soil should be due to different amounts of sunlight received between the two spots. A similar interpretation can be obtained from the analysis of the paired surface temperature measurements

(Figure 3.6). This shows the preferred model line becoming horizontal at 38°C. This could be interpreted as colonies actively avoiding sunny spots, in which soil surface temperatures approach 38°C.

Ecological Importance of Nest Location

It is becoming increasingly apparent that nest site selection plays a key role in a colony's ecological success. Ants can usually be ranked by their heat tolerance and their competitive ability (Cerdá et al. 1998a), and in general more competitive species are less heat tolerant (Cerdá et al. 1998b). The forest floor in BFL could become extremely hot when hit by direct sunlight, as temperature would commonly surpass 40°C and occasionally reach 50°C (Figures 3.5 and 3.6). Given that *P. dentata* activity occurs 24 hours a day, even in the hot season, a colony nesting in such a location would be faced with at least two challenges at the surface and the nest.

First, workers might be susceptible to heat fatigue if exposed to high temperatures for too long (Wehner et al. 1992, Cerdá and Retana 2000). Scouts are constantly searching for food through the leaf litter, and if a nest is located in an area highly exposed to sunlight it could prevent scouts from leaving the nest or it could force workers to forage near their critical thermal limits and increase their risk of death (Cerdá et al. 1998a, Wiescher et al. 2011). Fewer scouts searching for food could mean fewer discoveries of food resources (Wiescher et al. 2011). Although *P. dentata* is a fairly good competitor in Florida communities (Wiescher et al. 2011), it has a fairly low maximum abundance temperature and foraging thermal limit (27.4°C and 38.8°C respectively). Interestingly, *P. dentata* colonies in our Texas study site avoided nesting

in places if their surface temperatures exceeded 38°C (Figure 3.6). By remaining in shaded and cooler areas, *P. dentata* colonies might increase their competitive ability by allowing scouts and foragers to leave the nest earlier in the afternoon, and continue foraging later in the morning.

Second, mass recruitment by *P. dentata* might function less efficiently in hot soil surfaces. In mass recruiting species like *P. dentata*, scouts use recruitment pheromones to quickly guide foragers to food sources when the food item is too big to be carried by a single worker alone (Hölldobler and Wilson 1990). These pheromones are made of volatile hydrocarbon molecules (Morgan 2009) and recent experiments have shown that evaporation rates change on different substrates (Jeanson et al. 2003) and when substrates differ in temperature (van Oudenhove et al. 2011). Nest location could be crucial for the foraging success of a colony if it determines whether a colony will be able to forage or not because the sun is heating its nest's surface or its surroundings. Again, the fact that *P. dentata* colonies avoid nesting in locations that exceed 38°C might mean that recruitment above these temperatures is hindered by high evaporation rates of their recruitment pheromones. More research is needed to differentiate whether this temperature nesting limit is due to effects inside of the nest, effects on workers themselves while foraging, due to an increase in pheromone evaporation rates, or because of a combination of all these factors.

It remains to be understood what role soil humidity plays in colony site preference, and if the colony must trade-off between optimum levels of humidity vs. optimum temperatures. The costs associated with thermoregulation should be studied in the greater context of nest relocation, given that they are both tied together. Much is

understood about thermoregulation in land vertebrates, which allows them to sustain temperatures that are optimum for specific physiological, behavioral or ecological needs. In social insects thermoregulation may play a similar adaptive role as in vertebrates, yet cost/benefit analysis is still in its infancy.

Acknowledgements

We would like to thank Anthony Ho for his dedication helping collect field data in Texas. We are grateful to Larry Gilbert at the University of Texas in Austin and to John Crutchfield at Brackenridge Field Laboratory for generously allowing us the use of facilities at BFL. Tom Kursar, Fred Adler and Jon Seger gave insightful comments and suggestions. Funding was provided by the University of Utah, a National Science Foundation GK-12 Fellowship to M. M., and National Science Foundation grants DEB-0316524, DGE-0841233 and 10510-52352 to D.H.F.

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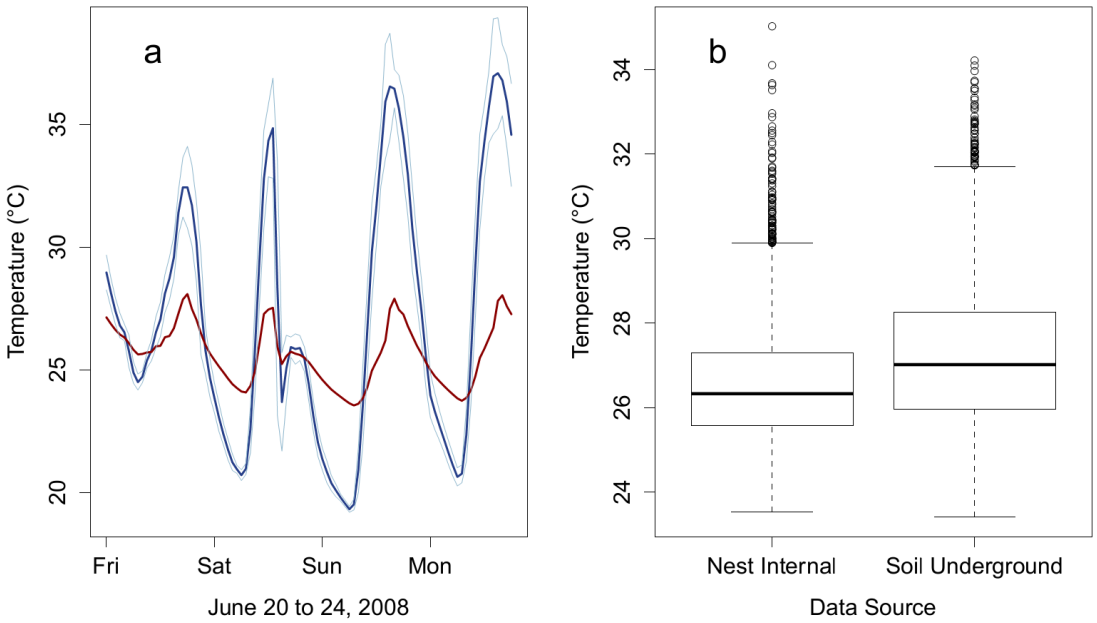

Figure 3.1**. a**. Comparison between average air temperature at BFL and typical internal nest temperatures at 5 cm below the soil surface. Data for this nest were collected from June 20 to June 24, 2008. The average temperature was lower than air temperature (25.56°C vs. 27.27°C). Blue line is average air temperature based on the average of four data loggers placed at BFL; light blue lines represent standard deviations. Red line represents nest temperature. **b**. Boxplots show all soil underground temperatures and all internal nest temperatures at 5 cm below the soil surface.

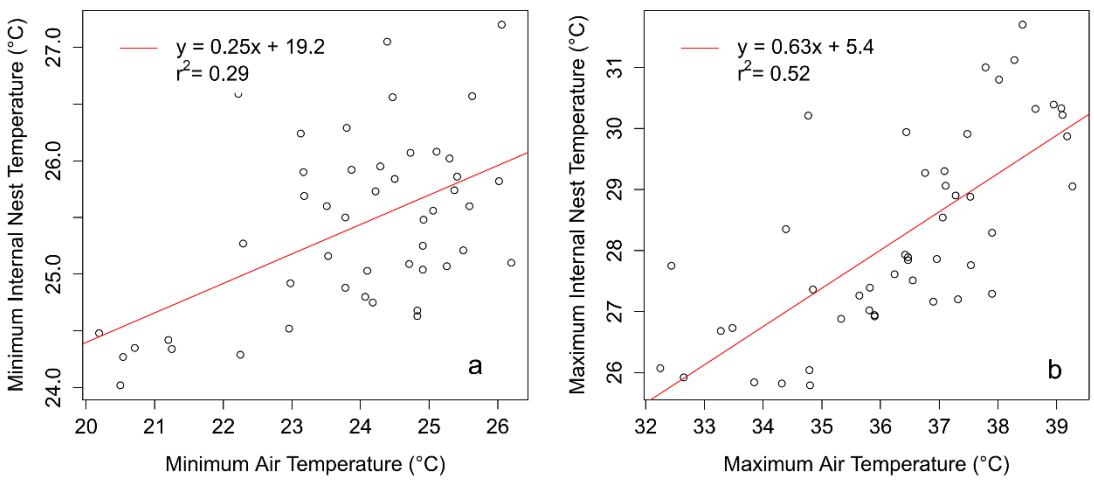

Figure 3.2. Regression between daily minimum internal nest temperature and MinAT in **a**, and daily maximum internal nest temperature and MaxAT in **b**. Two nests had internal temperatures monitored at any one time throughout the study period. Each ***y*** axis value represents the mean daily minimum (in a) or maximum (in b) of the two nests whose internal temperatures were monitored per day

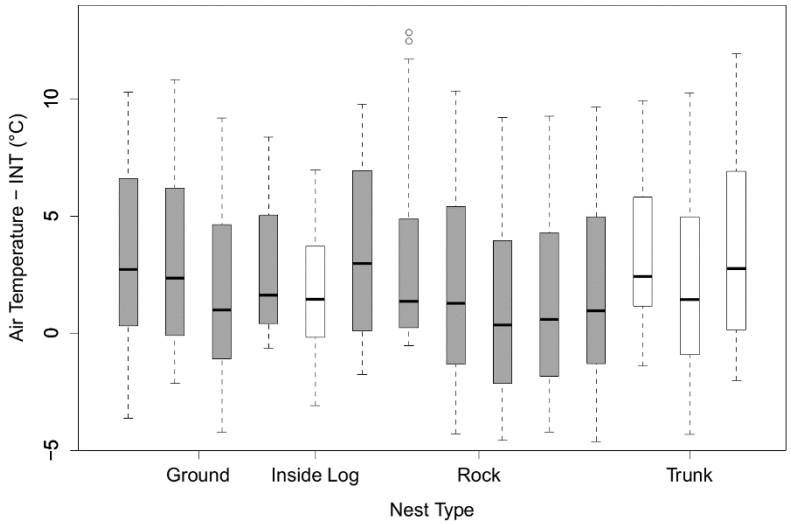

Figure 3.3. Boxplots of the temperature differences between nest readings and matching of simultaneous air readings; colors correspond to different nest types. All temperature recordings obtained during each hour of the day were averaged; 24 values were obtained per day for nest and air temperatures. A positive value means that air temperature was higher than nest temperature; negative values correspond to air temperature being lower than nest values.

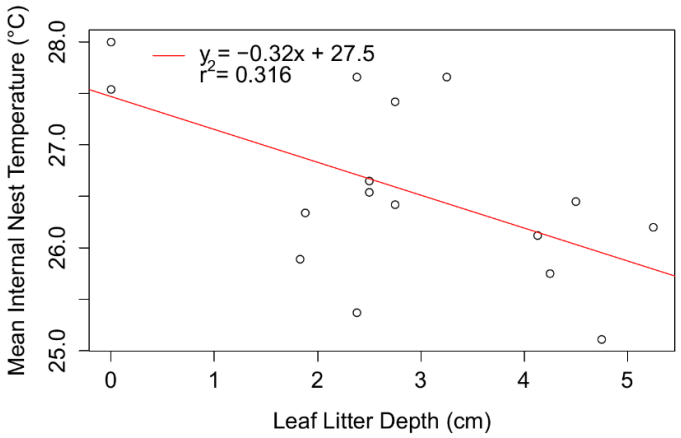

Figure 3.4. Regression between mean internal nest temperature and leaf litter depth (P = 0.0234).

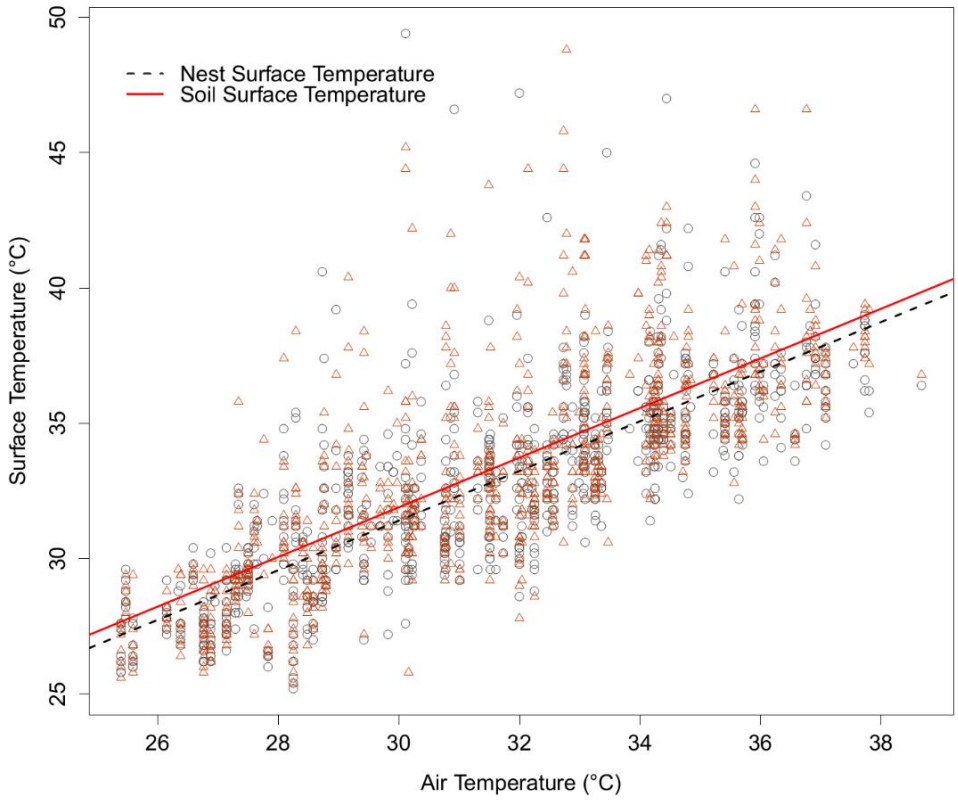

Figure 3.5. Relationship between the increase of surface temperature (based on infrared readings of soil surface) vs. air temperature. Surface temperatures above nest sites are represented by black circles; surface temperatures of the soil are represented by red triangles. Nest surface temperature slope (black dashed line) did not differ significantly from that of ground temperature slope (red line; *common slope* = 0.92, $F_{(1, 1750)}$ = 2494.6, P < 2.2e-16), yet surface temperatures of nests were on average 0.49°C lower than soil temperatures ($F_{(1, 1750)}$ = 17.74, P < 2.66e-05).

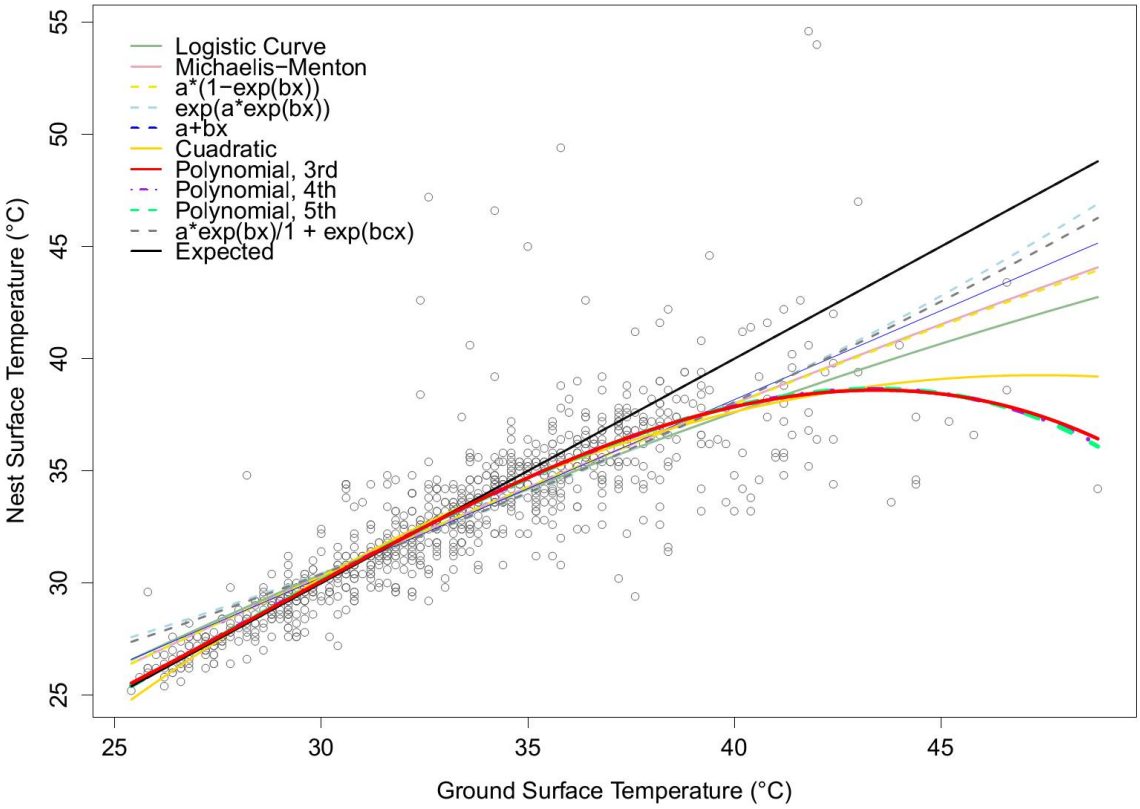

Figure 3.6. Relationship between surface measurements made with infrared thermometer of nest site and a random spot 1 m from the nest mouth. The regression lines of the different models are plotted against the data, plus the expected theoretical line with a slope of 1 (black line) that would occur if nests warmed up the same amount as the paired area. The best fit model is the 3rd order polynomial regression, which had the lowest AIC value (red line).

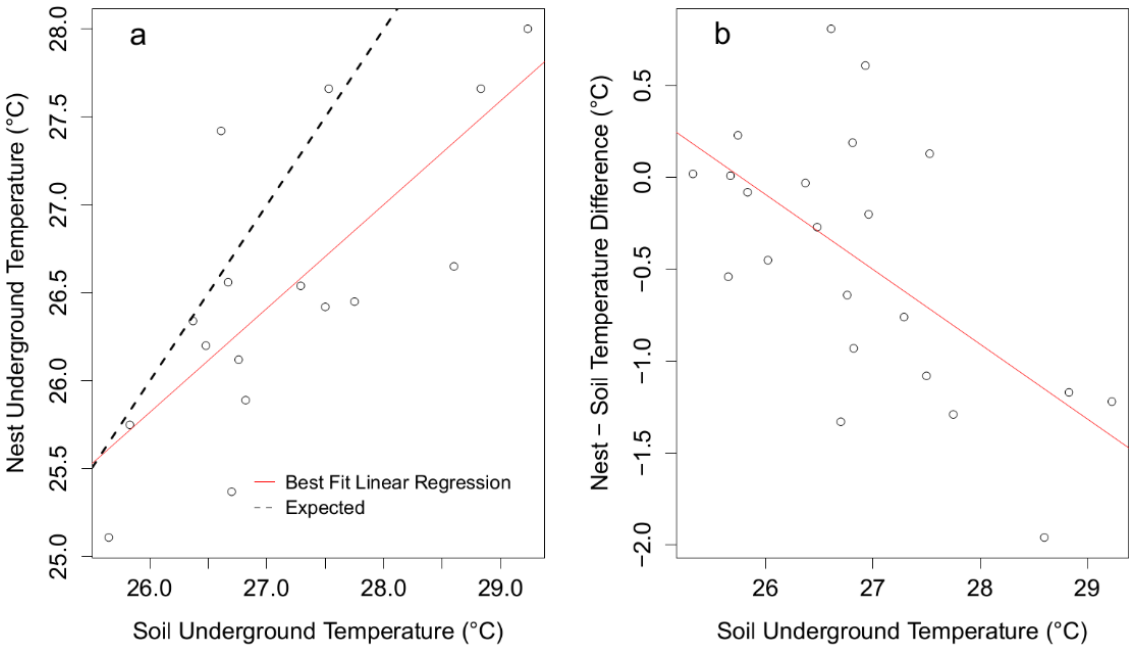

Figure 3.7. **a**. Relationship between paired internal nest temperatures (INT) and underground soil temperatures (UST). Red line represents the best fit line (*slope* = 0.59, *P* = 0.0011); the dotted line (with slope of 1) represents the expected line if no temperature difference occurred between nest and soil temperatures. **b**. Regression between UST and the difference between INT and underground soil temperatures (*Slope* = -0.41, *P* = 0.0027).

Table 3.1. ANOVA results of the effects of nest type on internal nest temperatures of nests.

	df	Sum Sq.	Mean Sq.	F Value	*P*
Nest Type	2	1.9647	0.9823	1.4075	0.2893
Residuals	10	6.9790	0.6979		

Table 3.2. Comparison of different models fitted against paired surface temperatures, using AIC. The best fit model corresponds to a 3rd order polynomial regression. dAICc is the difference in AIC value between the best model and the alternative model. df is degrees of freedom. Weight represents the relative likelihood of a model.

Model	dAICc	df	Weight
Polynomial, 3rd order	0	5	0.701
Polynomial, 4th order	2.6	6	0.186
Polynomial, 5th order	4.1	7	0.091
Quadratic	7.0	4	0.021
a·(1 - exp(bx))	67.1	3	<0.001
Logistic	68.4	3	<0.001
Michaelis-Menton	69.1	3	<0.001
Linear	92.6	3	<0.001
a·exp(bx)/(1 + exp(bcx))	149.7	4	<0.001
exp(a·exp(bx))	170.7	3	<0.001

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CHAPTER 4

RESOURCE DISCOVERY IN THREE ANT COMMUNITIES OF SPAIN

Abstract

The majority of ant species are omnivorous, having overlapping diets. This situation leads to high levels of competitive interactions among species at food resources. The dominance-discovery trade-off hypothesizes that species will differ along two axes, with some being good at discovering resources at the expense of being good at dominating resources, and vice-versa. How species differ in their discovery ability and through which mechanisms they are different remains poorly studied. In this chapter I report on resource discovery in Doñana, Grazalema and Cazorla, three local ant communities of southern Spain. Average discovery times differed in each community, with the costal location of Doñana having the fastest discovery time, and the highest location, Cazorla, the slowest. At the community level, more scouts searching for food meant faster discovery time (regardless of species identity). More scouts also meant faster discovery time at the species level for 12 out of 16 species studied. Discovery time was also determined by species-specific scout discovery capacity, or how quickly an individual ant finds food. For species with good individual

discoverers, each additional scout reduced discovery time disproportionately more than an additional scout of a bad discoverer did. Finally, *Aphaenogaster senilis* and *A. iberica* discovered food at higher temperatures than other species in all three communities. These results underscore that, at the species level, discovery depends on the number and the quality of scouts.

Introduction

All animals need food for survival, and many species need to continuously search for sources that are typically unpredictable in space and time (Pyke et al. 1977). Species have evolved different foraging strategies to harvest these food sources, which in turn are thought to influence the structure and dynamics of local communities (Kotler and Brown 1988). For instance, resource partitioning has been proposed to explain species coexistence in communities of Darwin's finches (Schluter and Grant 1984), sparrows (Pulliam 1985), and coastal diving birds (Holm and Burger 2002). Habitat specialization may explain coexistence in desert rodents (Kotler and Brown 1988, Brown et al. 1994) and the use of different foraging strategies likely reduces competitive interactions in ants (Johnson et al. 1987, Cerdá et al. 1998b). Given that particular foraging strategies require certain adaptations (Price 1987), species are likely to face trade-offs that limit their ability to dominate resources (Kotler and Brown 1988). For example, Darwin's finches face a trade-off with respect to the seeds they are best able to consume: larger beaks allow for better handling of large seeds, yet makes eating small seeds more cumbersome. The reverse is true for birds with small beaks, which

makes eating small seeds easier, yet more difficult to crack open the larger seeds with a harder shell (Schluter et al. 1985, Price 1987, Grant and Grant 2006).

The question of how ant species diversity is maintained in a local community is still one of intense debate and research in ecology. In temperate communities, few ant species are dietary specialists (Hölldobler and Wilson 1990). Instead the majority of species are omnivorous and their diet broadly overlaps, feeding on a mixture of animal and plant sources, such as insect prey, seeds and honeydew (Fellers 1987, Mooney and Tillberg 2005, Valone and Kaspari 2005). This dietary overlap translates into potentially intense competitive interactions at food sources, and several ecologically based trade-offs have been proposed to explain species coexistence in ants (Cerdá et al. 1998a, Davidson 1998, Feener 2000, Lebrun and Feener 2007b, Cerdá et al. 2013). One of them, the dominance-discovery trade-off, suggests that species can specialize in finding food rapidly or enlist large numbers of recruits to defend food sources, but they cannot do both (Fellers 1987, Savolainen et al. 1989, Andersen 1992, Holway 1999, Feener 2000, LeBrun 2005). This comes about as a result of the limited number of ants in a colony: there will necessarily be a trade-off in workers allocated to search for food and workers allocated to stay in the nest to be recruited. This trade-off predicts that species that invest heavily in scouts should discover and remove small food items before competing species that invest heavily in recruits can find and usurp them.

Finding food is costly for colonies, as foragers have a much higher mortality risk when outside the nest, due to predation (Whitford and Bryant 1979), heat (Wehner et al. 2004, Wiescher et al. 2011), desiccation and disorientation. On the other hand, energy costs incurred by a worker during travel and food transportation are small compared to

potential energy intake (Weier and Feener 1995). Rather, it is likely that calorie consumption by colonies is limited by the amount of available search time (Fewell 1988, Morehead and Feener 1998) and the inefficiencies incurred by a number of foragers looking for food simultaneously (Johnson et al. 1987). How species in a community differ in their discovery strategies is likely to have considerable ecological implications, as this might be one of the mechanisms underpinning species coexistence. To date research on foraging in ants has largely focused on resource dominance (Fellers 1987, Savolainen and Vepsäläinen 1988, Andersen 1997, Cerdá et al. 1998c) and our understanding of species discovery ability is limited. For example, it is not well known whether species differences in resources discovery are the results of colony differences in the number of foragers or whether individual foragers differ in their discovery ability. Recent studies have begun to shed some light on these questions. In local ant communities in Texas and Arizona, the total number of foragers predicted discovery time at the community and species level (Pearce-Duvet et al. 2011b). Also, the discovery ability of individual foragers differed by species, as foragers of some species were more efficient at discovering food than others (Pearce-Duvet et al. 2011b). Species also varied in their response to abiotic factors, such as vapor pressure deficit (VPD).

Our aim in this study was to extend our understanding of discovery ability in ants by studying three communities in Spain. Dominance in Spanish ant communities has been well studied (Cerdá et al. 1997, Cerdá et al. 1998a, Cerdá et al. 1998c, Retana and Cerdá 2000), yet discovery dynamics are not well understood. These communities thus represent an ideal study system that will allow us investigate whether the ecological patterns found in North America are present in Iberian communities. To

address these objectives, we compared resource discovery in these three local communities and whether species differed in their discovery ability at these different localities. We also examined the influence of environmental conditions such as ambient temperature and VPD on discovery ability of individual species.

Materials and Methods

Study Sites

We carried out our study at 3 different locations in southern Spain: Parque Nacional de Doñana (36°59'22"N, 6°26'36"W), Parque Natural de las Sierras de Grazalema (36°46'43"N, 5°23'56"W), and Sierras de Cazorla (37°56'51"N, 2°52'41"W). At each location 2 plots were set up for data collection. Sampling occurred in the months of April, May and June, respectively.

Doñana is a coastal area of sandy dunes and wetlands located at the delta of the Guadalquivir River to the Atlantic Ocean (elevation < 10 m). It has a Mediterranean climate, with wet winters and dry summers (mean annual precipitation is 462 mm). The mean annual temperature is 19.2 °C, with July being the warmest month (mean temperature of 27.3°C), and January the coldest (mean temperature of 11.9°C). Vegetation at the 2 plots consisted mostly of shrubs and herbs, with open areas of sandy soil.

Grazalema sites were located in the Sierras del Pinar (elevation ~ 1000 m), approximately 5 km northwest of the city of Grazalema. One plot was located under an open, mixed canopy forest, consisting of pines and oaks. The second plot was located under an open pine forest. Grazalema is located in the most humid region of Spain, with

annual precipitation between 1200 and 2000 mm, mostly restricted to the winter months. Mean monthly temperatures are 12.8°C in January and 20.9°C in August.

Cazorla plots were located near the Roblehondo Field Station (elevation ~ 1330 m). This location has a Mediterranean climate, with moderate, dry summers and cool, humid winters. Precipitation is approximately 1000mm/year. One plot was located under a mixed pine (*Pinus nigra*) and oak forest, and the second plot was situated in an open, grassy meadow.

Experimental Design

Each plot consisted of 25 stations arranged in a 5 x 5 grid, with stations separated by 10 m. Plots covered approximately 250 m^2 and each station was marked by a flag. Our experimental procedure consisted of a 2-step process.

First step. To obtain an estimate of the local abundance of ant foragers prior to baiting, a 0.25 m^2 circular hoop was placed at each station on the ground. For a total of 5 minutes, all the ants observed inside the hoop were counted, and their species visually identified. If we were unable to identify the species in the field, a sample was collected for later determination in the lab. Ants belonging to a foraging trail or returning to the nest with food were not included in the count.

Although the use of hoops to estimate the number of scouts looking for food is relatively novel (see Pearce-Duvet et al. 2011), there are advantages with this method that make their use worthwhile. Prior methods to estimate forager density relied on pitfall-traps set throughout the study area. These traps are typically left open for 24 hours, during which time they collect insects, including ants, that fall in the cups. Pitfall

traps provide good assessments of the local ant assemblage (Andersen 1991), yet they are unable to give short-term densities that we needed for this study. Hoops, meanwhile, provide a good snapshot of the forager identity and abundance just prior to setting the bait. Hence, hoops allow for a good resolution of forager dynamics at spatial and temporal scales. They nevertheless have drawbacks. The timescale of hoop counts are of short duration, and spatially restricted. This suggests that hoop counts should be repeated in time and through relatively large area, to insure a meaningful sampling of local conditions.

Second step. At the end of the 5 minutes, the hoop was removed, and a bait was placed on a 9 cm diameter white plastic card in the center of the hoop. Baits consisted of a 3 to 4 mm thick slice of hot dog frank. Hot dog baits were a mixture of lipids, carbohydrates and protein (11:3:4 mass ratio) with 11 mg sodium/g and were successful at attracting a wide variety of ants. Baits were observed until they were discovered or until 1 hour had passed. The time to discovery by an ant and its identity was recorded. We defined time to discovery as the time it took from the moment the bait was set on the ground until an ant made physical contact with the bait. Each plot was sampled twice. Trials were carried out during times of maximum ant activity in all three communities, between 9:00 and 20:00 hours.

At each station, temperature and air relative humidity were measured prior to hoop counting, using a handheld meter (Oacton®) placed at ground level. At the moment of bait discovery, the surface temperature of the baiting card was measured using an infrared thermometer (Meterman® IR608).

Statistical Analyses

Survival analyses. All our analyses were carried out in R 2.15 (R Development Core Team 2013). We performed analyses at the level of each ecological community and at the level of individual species within each ecological community. First, to determine if the average number of ants in hoops differed significantly in each community, we ran a generalized linear model, using a Poisson distribution, with total number of ants in hoops as response variable, and community as predictor variable. Second, we fitted an exponential curve between discovery time as response variable and number of foragers as predictor variable, using a nonlinear regression. Individual models were run for each community (Figure 4.1). Third, to obtain an estimate of the mean discovery time we calculated Kaplan-Meier curves for each community. These curves, as opposed to Cox proportional-hazard models, provide median discovery times (but no statistical tests). Fourth, to statistically test survival time differences between the three communities, we ran an overall survival analysis using a Cox proportional-hazards (CPH) regression model. In this analysis we included discovery time as response variable, and the following factors as predictor variables: total number of ants present in hoops (regardless of species), community, and the temperature recorded at the moment of species count in the hoop. We reduced the full model with interactions using backward elimination of variables.

We also ran independent CPH analyses at the species level. For these analyses, we included species that had been observed in hoops at least 8 times, and discovered the bait at least twice, otherwise the power of the analysis was too small to discern an effect. Although we could not include the majority of species found in hoops, the

species that we did include comprised 90%, 97% and 81% of the discoveries in Doñana, Grazalema and Cazorla, respectively. The models included number of foragers and temperature at the moment of discovery as predictor variables. Full models for each species were reduced via backward variable elimination. These analyses provided us with a species-specific rate of discovery we called the per capita coefficient (PCC). This rate tells us how good a single forager is at discovering food. Foragers with PCC values greater than zero have shorter discovery times compared to foragers with PCC values less than zero.

To control for multiple sampling at the same stations, we included frailty in our survival analyses models, which reduces the potential effects of autocorrelation in our data (Therneau et al. 2003).

We explored the ability of each species to discover resources by comparing their probability of discovery. For this, we counted the number of times a species had been observed at a hoop in each community (maximum 25x2x2=100 times), which we called the Number of Occurrences (NO). We then counted the number of times a species had discovered the bait given that it was present in the hoop before the discovery, which we named Number of Discoveries (ND; maximum $\leq$ NO). Probability of discovery was calculated as ND/NO. This method controls for species relative abundance, given that species present in a hoop were potentially able to locate the food source first, and is similar to methods in other studies that used pitfall traps for its estimation (LeBrun and Feener 2007a).

We tested whether species might trade-off traits such as PCC, NO and probability of discovery, given that investment into these traits might come at a cost to

colonies, and species might specialize on one of them while unable to invest in others. We carried out correlations at the community level to explore this hypothesis.

Abiotic specialization of foragers. We compared temperature preferences of ant species in 2 ways. First, species might differ in their preferred foraging temperatures, that is, species might restrict their foraging activity to particular daily temperatures. We therefore compared species at the community level through a linear model, using number of ants in a hoop as the response variable and species x temperature interaction as the explanatory variable. We called this the average foraging temperature (AFT). Second, species could also vary in their average temperature of discovery, i.e., the average air temperature at which baits are discovered. We tested this hypothesis by comparing temperature at the moment of discovery for each species with a linear model, using discovery temperature as the response variable and species as explanatory variable.

Results

Community Level Results

The Kaplan-Meier analysis shows that Doñana was the community with the shortest overall discovery time, with a median of 5.0 minutes (95% CI = 2.8-8.3 minutes), significantly shorter than Grazalema (median = 6.9 minutes; 95% CI = 5.8-8.7 minutes; coefficient = 0.44, $\chi^2 = 5.1$, P = 0.02), and Cazorla (median = 7.4 minutes; 95% CI = 6.1-9.2 minutes; coefficient = 0.73, $\chi^2 = 10.3$, P < 0.01). The overall analysis at the community level, based on the Cox proportional-hazards model, agrees, showing that discovery time in Grazalema was significantly slower than in Doñana (Table 4.1).

There was a significant interaction between Cazorla and number of foragers. This shows that, in Cazorla, additional scouts searching for food decrease discovery time, but less effectively than what adding a forager in Doñana would do to discovery time (Table 4.1). The number of foragers in hoops (regardless of species identity) significantly reduced discovery time in all three communities (Table 4.1 and Figure 4.1). There was a negative relationship between discovery time and ambient temperature. In addition, communities differed in the number of foragers found in hoops (Poisson generalized linear model estimates: Doñana: mean = 4.1 ± 0.2 ants, Z = 20.3, $P < 0.001$; Grazalema: 6.0 ± 0.3 ants, $Z = 5.8$, $P < 0.001$; Cazorla: 7.9 ± 0.4, $Z = 10.5$, $P < 0.001$). The number of ants in hoop explained 51% of the variation in time to discovery in Doñana, 7.8% in Grazalema, and 32.5% in Cazorla.

Species Level Effects: Forager Numbers on Time to Discovery

We recorded 17 species discovering baits in Doñana, 13 species in Grazalema and 23 species in Cazorla. From these we could obtain statistically meaningful estimates for four species in Doñana, five in Grazalema, and six in Cazorla.

Kaplan-Meier analysis shows that species differed in their median discovery times (Table 4.2). *Aphaenogaster senilis* had the shortest discovery time in Doñana (median ~ 3 min), while *Plagiolepis pygmaea* had the longest discovery time (median ~ 15 min). The survival models show that, at the species level, the number of foragers in a hoop significantly correlated with time to discovery in 11 of the 15 species included in the analysis (Table 4.3). For these species, except orange *Leptothorax*, a greater number of foragers in the hoop decreased the discovery time of the bait. No relationship

between the number of foragers in hoop and discovery time was observed for *P. pygmaea* and r/b *Myrmicine* in Doñana, and in *Crematogaster sordidula* in Cazorla.

Species differed strongly in the proportion of baits that they discovered (Table 4.4). *Aphaenogaster* species discovered the majority of baits in all three communities. In Doñana and Grazalema *A. senilis* found 98% and 90% of baits, respectively, when a forager had been present in the hoop. In Cazorla, *A. iberica* found 77% of baits given that it was present in the hoop. Other species, in contrast, were poor discoverers, and found only a minority of baits: in Doñana, *Messor* and r/b *Myrmicine* found ~8% of baits. *P. pygmaea* found 18% of baits in Grazalema and *C. sordidula* found 14% in Cazorla.

In Cazorla there was no relationship between the mean number of foragers in hoops and the per capita coefficient (t = -2.7, P = 0.07, df = 4), nor was the proportion of discoveries related to the per capita coefficient (t = 1.549, P = 0.2192, df = 4), or mean number of foragers in hoop (t = -0.927, P = 0.406, df = 4). Lack of per capita coefficient estimates for all species in Doñana and Grazalema did not allow us to perform a similar analysis at these sites.

The Role of Temperature on Resource Discovery

Species did not show significant differences in maximum activity temperatures (MAT) in any community (Doñana: F = 1.4, P = 0.26, df = 3, 159; Grazalema: F = 1.03, P = 0.39, df = 4, 231 and Cazorla: F = 1.11, P = 0.36, df = 5, 185). In contrast, there were species-level differences in average discovery temperature (ADT; Figure 4.2). In Doñana, ADT was significantly different between *Aphaenogaster senilis* and

Crematogaster aubertii (ADT = 27.8°C vs. 24.6°C, respectively; t = -2.4, P = 0.02, df = 3, 79). In Grazalema, the average temperature of food discovery was significantly higher for *A. senilis* and *Formica* sp. than for orange *Leptothorax* (ADT = 30.7°C, 29.6°C vs. 20.4°C, respectively). In Cazorla, ADT of *Aphaenogaster iberica* (32.4°C) was significantly greater than that of all species, except for *Plagiolepis pygmaea*

For three species, the survival analyses showed that the per capita coefficient of discovery interacted with changing temperatures. In Grazalema, a positive interaction between forager numbers and discovery temperature is present for orange Leptothorax, which suggests that the discovery ability of foragers increases with temperature. This might occur because orange Leptothorax appears to specialize for foraging during the coldest part of the day (its ADT was 20.4°C), so increasing temperatures might benefit individual foragers more than they benefit foragers of other species. The reverse occurs with Cazorla ants *A. iberica* and *Camponostus cruentatus*. In these 2 species, there is a negative interaction between discovery temperature and number of foragers, suggesting that as temperature increases, the value to a colony of adding more foragers (in terms of reducing discovery time) decreases.

In Doñana, *A. senilis* found food significantly faster at higher temperatures, as measured by discovery temperature, although this effect did not occur in Grazalema, where it was also present. In contrast, *Leptothorax* ants foraged at the lower temperature end, either during the morning or the evening, but were absent during the hottest times of the day. For *A. iberica* in Cazorla there was also a significant interaction between forager number and temperature at the moment of discovery, which suggests that at

increasing temperatures the per capita rate of discovery is reduced. This could be due to foragers avoiding soil temperatures that surpass a critical temperature.

Discussion

The ecological success of ants is undoubtedly tied to foraging behaviors that allow colonies to harvest the continuous, but randomly located, stream of resources appearing around nests. Because most resources are short-lived, species must find food items before competitors do. This is especially true for subordinate species, which can potentially lose resources to more dominant species (Fellers 1987, Savolainen and Vepsäläinen 1988, LeBrun 2005). Given the social nature of ants, their strategies for resource dominance are diverse and relatively well studied (Traniello 1989, Cerdá et al. 2009). Yet the processes by which species find food remains largely unexplored. By studying resource discovery in three ant communities in Spain, we attempted to answer three basic questions: How do communities differ in their discovery dynamics? What strategies do species use during resource discovery? How do abiotic factors affect resource discovery at the community and species levels?

Forager Number and Resource Discovery

Theoretical research has proposed that discovery is a function of the number of ants looking for food (Johnson et al. 1987, Adler and Gordon 1992). In particular, an increase in their density should increase the likelihood that any ant will encounter a food resource (Gordon 1995), at both the community and the species level, yet these hypotheses have seldom been tested. Our results agree with these predictions, and show

that discovery time is negatively correlated with the overall number of ants in the vicinity of a food item. That is, the greater the total number of foragers, regardless of species, the shorter the time to discovery in these three communities. A similar pattern existed at the species level for the majority of ant species (Table 4.3), in which an increase in forager numbers reduced the time to resource discovery.

Given that our understanding of resource discovery in communities is limited, it is reassuring that these results share similar patterns to those found by Pearce-Duvet et al. (2011b). In their study, an increase in the number of ants reduced discovery time in 2 ant communities of North America, and this effect existed at the species level as well. In both studies there is great variation in the discovery ability of individual foragers as well (Table 4.3 in this study, Table 2 in Pearce-Duvet et al. (2011b)). This suggests that discovery at the community level is a complex interaction of number and quality of foragers searching for food.

If foragers of all species were ecologically equivalent in terms of their ability to find food, then the proportion of baits discovered by species is expected to be a function of their relative nest abundance, given that nest abundance varies by species (Kaspari 1993). In our study, forager number explained some of the variation of discovery time, yet a large portion remained unexplained (51% of the variation in time to discovery in Doñana, 7.8% in Grazalema, and 32.5% in Cazorla). We can observe this if we compare the average number of ants in hoops in each community with the respective median discovery time. Doñana, with the lowest average number of foragers (4.14 ± 0.2 ants), had the fastest discovery time. Discovery time was longest in Cazorla, which also had the highest mean number of foragers. This suggests that species identity is as important

in understanding discovery dynamics at the community level as is the total number of foragers.

The faster discovery rate in Doñana, despite having a lower mean number of foragers in hoops, could be due partly to the ability of *A. senilis* foragers in finding food. Workers are large and move fast through the terrain (Cerdá et al. 2009), traits that might aid in resource discovery (Pearce-Duvet et al. 2011a). In fact this species had the shortest discovery time (median = 3 min) of all ants in our study. *A. senilis* was also the most abundant in the community, as measured by the number of occurrences in hoop surveys (Table 4.1). Moreover, it discovered baits numerous times even when it had not been observed in the hoop during our survey. All this could make *A. senilis* have an inordinate effect on resource discovery, lowering average discovery time for the entire community. Although *A. senilis* was also abundant in Grazalema, its median discovery time did not differ greatly from the other species in this community. This result is intriguing, as it suggests that a single species could establish a benchmark upon which all other species must compete. Some of our data hints at this possibility: the median discovery time for *A. senilis* is 2 times greater in Grazalema compared to Doñana (6 min. vs. 3 min); a similar pattern occurs with *P. pygmaea,* whose discovery time doubles from 6 min, in Doñana, to 15 min in Grazalema. These results agree with previous theoretical work on the dominance-discovery trade-off by Adler et al. (2007). In their model they showed that dominant species, with slower discovery times, are more susceptible to the effects of fast discoverers than fast discoverers are affected by dominant species. The slower a species is at finding food, the more likely it will go extinct while the best discoverer will always persist. If indeed *A. senilis* is setting the

pace for these communities, then its faster discovery time may make coexistence more difficult for slow discoverers in Doñana than in Grazalema. This suggests that much remains to be learned about competition and coexistence of ant communities.

The Dominance-Discovery Trade-Off

Numerous theoretical studies investigated optimal foraging in social insects with respect to the division of labor in nests between scouts that search for food and recruits that wait in the nest for information about food sources before actively participating in foraging (Johnson et al. 1987, Dechaume-Moncharmont et al. 2005). It has generally been recognized that small colonies will prefer solitary or group foraging (Beckers et al. 1989), thus investing the majority of their work force into scouts (Johnson et al. 1987, Jaffe and Deneubourg 1992). Larger colonies should invest more heavily in recruits (Beckers et al. 1989), as this would provide the colony with the ability to defend food items and harvest clumped or large resources rapidly. These different strategies should translate into different discovery times. Subordinate species, with a greater foraging force, should be able to discover resources sooner. In small honey-bee colonies, foraging success was similar to that of larger colonies (Beekman et al. 2004), suggesting that increasing the number of foragers might help colonies find resources faster, yet adding more foragers will have diminishing returns as workers will begin to overlap in their research territories (Naug and Wenzel 2006). In this context, small colonies might be able to survive even in proximity to and dominant species with larger colonies.

Our results generally support these predicted trends. The best discoverers are solitary or group foragers (*Aphaenogaster* spp., *Camponotus cruentatus*), while slower discoverers are mass recruiters (e.g., *Pheidole pallidula*, *Crematogaster aubertii or Forelius sp.*). Nevertheless, there were some exceptions that did not fit neatly into this model. For example *Plagiolepis pygmaea* is a submissive ant and a group forager (Cerdá et al. 1997), yet it consistently ranked as a slow discoverer and low in the proportion of baits found. This species is also risk-averse, foraging at comparatively low temperatures, when behaviorally dominant species are more active (Cerdá et al. 1998a). It is probable that other trade-offs are operating in the community, which is enabling *P. pygmaea* to survive. It remains to be seen how this species is able to successfully coexist in these ant communities.

Our data suggest that species with small colony sizes, such as *Aphaenogaster iberica* and *A. senilis*, might invest resources differently than species with larger colonies, such as *Pheidole pallidula*. For a small colony, maximizing energy intake might mean investing in foragers capable of fast discovery (Pearce-Duvet et al. 2011a, Pearce-Duvet et al. 2011b), providing a competitive advantage against dominant species. For large colonies, with an abundant workforce available, investing in workers able to win during interactions with other ants might be more advantageous (Holway 1999, Dornhaus et al. 2006). Efficient foragers should be particularly important for small colonies, which are likely to encounter greater variability in their foraging success compared to larger colonies (Naug and Wenzel 2006). This pattern has also been observed in both North American communities studied by Pearce-Duvet et al. (2011b)

Abiotic Effects on Foraging

Discovery temperature was a good predictor of time to discovery at the community level at all three sites. When temperature increased, time to discovery decreased. Higher temperatures might increase the walking speed of ants and shorten discovery times. The walking speed of ants depends on body temperatures (Hurlbert et al. 2008), and an ant's temperature closely follows soil temperatures (Wehner et al. 1992). Thus, discovery at the community level will be subject to the ambient temperatures and the species-level differences in response to temperature. Species respond differently to changing temperatures by several mechanisms, including running speed (Hurlbert et al. 2008), activity levels (Cerdá et al. 1997), and physiological responses (Cerdá et al. 1998a, Wiescher et al. 2012). Thus, the effect of temperature on discovery ability is likely to vary among ant species and variation in their relative abundance should influence the effect of abiotic temperature on resource discovery at the community level.

We have some evidence for this in our current study. In Doñana, *Aphaenogaster senilis* appeared to take advantage of warmer temperatures, as temperature correlated inversely to its time to discovery. These results agree with previous studies that show *A. senilis* as a risk-prone species that forages close to its critical thermal limit, presumably because its foraging efficiency increases with temperature (Cerdá et al. 1998a, Cerdá et al. 2009). In Grazalema, orange *Leptothorax* showed a positive interaction between the number of foragers and temperature, suggesting that its efficiency increased disproportionally with temperature. This is peculiar, since orange *Leptothorax* appears to be a cold specialist, discovering baits at the lowest discovery temperature of all ants

(mean = 20.4°C ± 3.3°C). While this species might benefit from warmer temperatures, this benefit is likely restricted while temperatures are relatively low; at temperatures higher than 25°C, this species discovered baits only a few times.

In Cazorla, temperature produces an intriguing effect on the foraging efficiency of *Aphaenogaster iberica* and *Camponotus cruentatus*. The individual survival models show a negative interaction between number of foragers and temperature. This suggests that foraging efficiency decreases at higher temperatures. If foragers are able to cover more surface area at higher temperatures because of their faster speed, then increasing forager numbers when temperatures are high will produce diminishing returns to the colony. This could result from foragers starting to duplicate their searching territories, reducing the value of each added ant (Gordon 1995).

The problem of how ant communities are assembled has been a long-standing question in community ecology (Cerdá et al. 2013). Starting with studies on interspecific interactions in the 1980's, it was apparent that, in many communities, species followed a dominance hierarchy (Fellers 1987, Savolainen and Vepsäläinen 1988, Holway 1999). An emphasis has been given in understanding how dominant species affect the survival of less dominant ants. Nevertheless, in this and previous studies (Pearce-Duvet et al. 2011b), we show that resource discovery is as crucial in understanding community dynamics as is dominance of those resources. Together with theoretical research (Adler et al. 2007), a different picture emerges which suggests that good discoverers might outcompete other species unable to find resources fast enough. This would make ant communities different than those of plants, in which subordinate species do not affect more competitive species in the competition-colonization trade-off

(Tilman 1994). Comparative studies between ants and plants might point to the mechanisms of coexistence working in each assemblage. Although the behaviors are different, the patterns that emerge in ants and plants are similar.

Acknowledgments

We would like to thank Xim Cerdá, without whose invaluable help our work in Spain would have been impossible. Raphaël Boulay kindly identified ant specimens. Tom Kursar, Fred Adler and Jon Seger gave insightful comments and suggestions. Funding was provided by the University of Utah, a National Science Foundation GK-12 Fellowship to M. M., and National Science Foundation grants DEB-0316524, DGE-0841233 and 10510-52352 to D.H.F.

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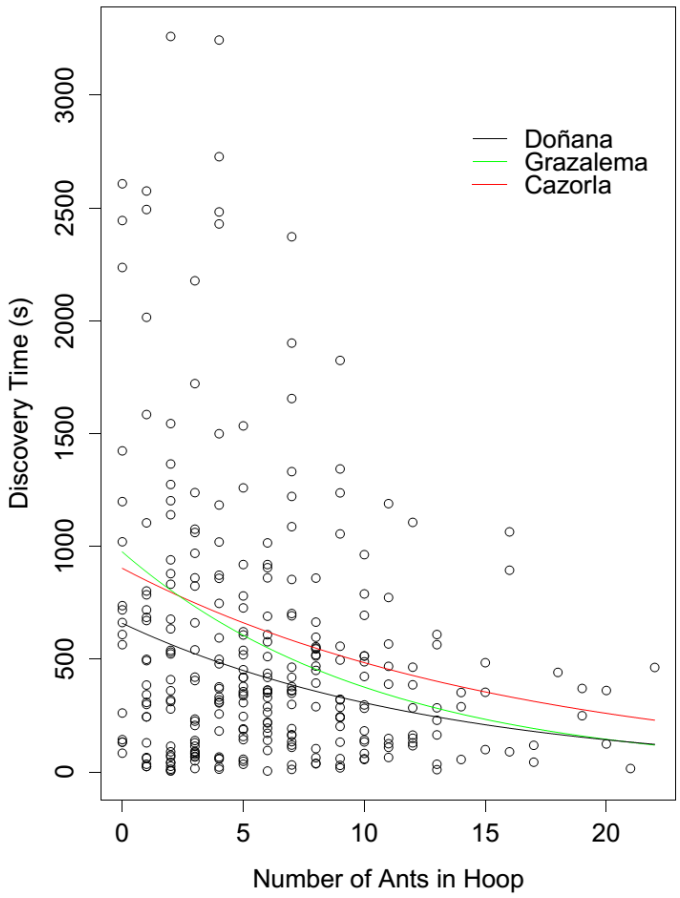

Figure 4.1. Discovery time as a function of the number of foragers in hoops for Doñana, Grazalema and Cazorla communities. The curves follow a negative exponential line.

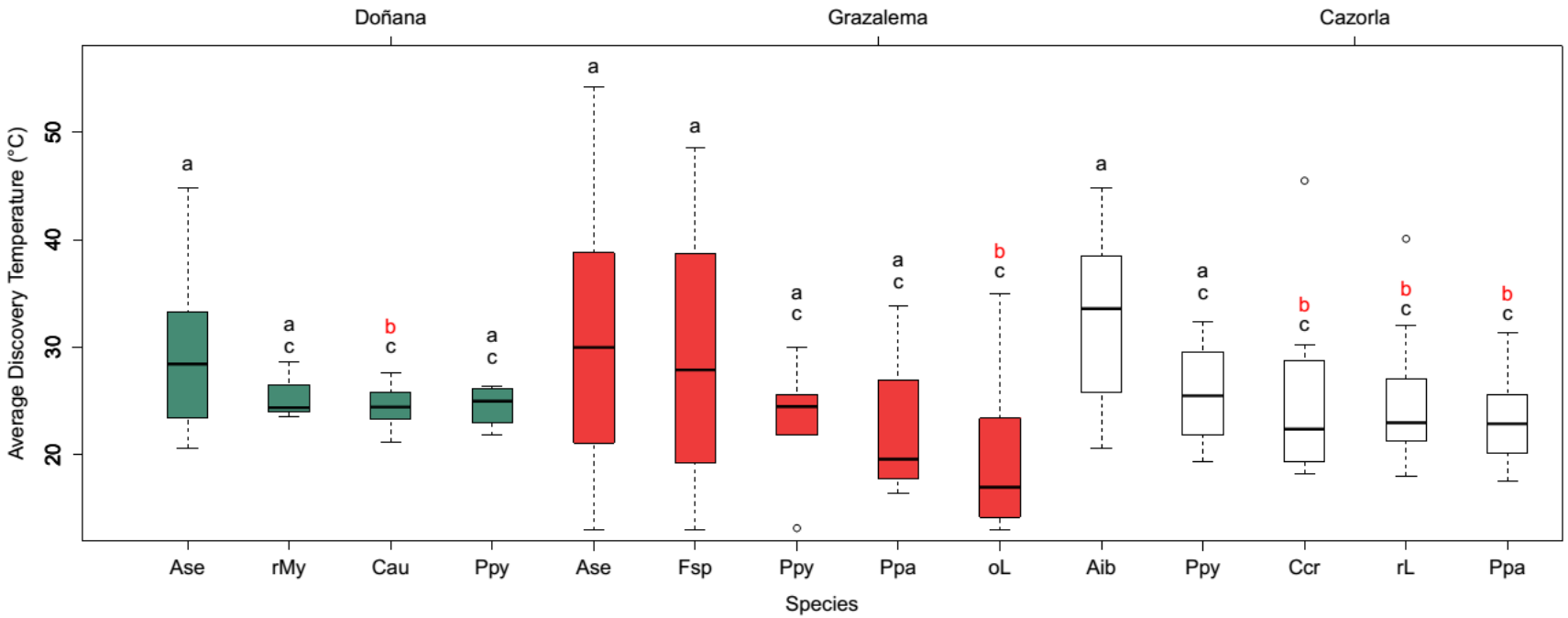

Figure 4.2. Boxplots of discovery temperatures by species. Species within a community that do not share the same letter discovered baits at significantly different temperatures. The middle black line of boxes represents median temperatures, the lower and higher ends of boxes the 25% and 75% quartiles, respectively. The species abbreviations are as follows: Aib, *Aphaenogaster iberica*; Ase, *Aphaenogaster senilis*; Ccr, *Camponotus cruentatus*; Cau, *Crematogaster aubertii*; Fsp, *Forelius* sp.; Ppa, *Pheidole pallidula*; Ppy, *Plagiolepis pygmaea*; oL, orange *Leptothorax*; rL, r/b *Leptothorax*; rMy, r/b *Myrmicine.*

Table 4.1. Results of survival analysis based on Cox proportional-hazards regression model. The main effects were location, number of foragers and temperature at the moment of discovery.

Main Effects			Foragers x Location Interaction	
	Coefficient	*P*	Coefficient	*P*
Cazorla			-0.24 ± 0.07	0.0008
Grazalema	0.30 ± 0.24	0.02		
Foragers	0.30 ± 0.06	0.000		
Discovery Temperature	0.03 ± 0.009	0.001		

Table 4.2. Median discovery times of species from a Kaplan-Meier survival analysis. Records are the number of observations for each species.

Species	Records	Median (sec)	Median (min)
Doñana			
Aphaenogaster senilis	66	178	2.97
Crematogaster aubertii	10	580	9.67
r/b Myrmicine	2	338	5.63
Plagiolepis pygmaea	4	360	6.00
Grazalema			
Aphaenogaster senilis	56	358	5.97
Crematogaster scutellaris	2	578	9.63
Forelius sp.	16	485	8.08
orange Leptothorax	13	490	8.17
Plagiolepis pygmaea	6	920	15.3
Cazorla			
Aphaenogaster iberica	11	343	5.72
Camponotus cruentatus	11	470	7.83
Pheidole pallidula	16	362	6.03
Plagiolepis pygmaea	4	408	6.80
r/b Leptothorax	31	498	8.30
Crematogaster sordidula	2	143	2.38

Table 4.3. Summary of species-level traits. Number of occurrences refers to the number of times a species was observed in a hoop in each area. Number of discoveries is given that the species had been observed in the hoop. Mean foragers is the average number of foragers when they were present in hoops. The per-capita coefficient comes from the species-level survival models and refers to the ability of foragers to find food (greater values mean better discoverers).

Species	No. Occurrences	No. Discoveries	Proportion Discovered	Mean Foragers	Per Capita Coefficient
Doñana					
Aphaenogaster senilis	42	41	0.98	2.52 ± 0.33	0.31 ± 0.06
Cremastogaster aubertii	33	15	0.45	3.33 ± 0.42	0.30 ± 0.09
Plagiolepis pygmaea	33	5	0.15	2.15 ± 0.19	NA
r/b Myrmicine	14	1	0.07	1.64 ± 0.23	NA
Grazalema					
Aphaenogaster senilis	42	38	0.90	1.64 ± 0.15	0.77 ± 0.12
orange Leptothorax	32	21	0.66	2.53 ± 0.4	-0.53 ± 0.38
Crematogaster scutellaris	18	8	0.44	2.61 ± 0.57	NA
Forelius sp.	41	14	0.34	2.41 ± 0.26	0.60 ± 0.15
Plagiolepis pygmaea	49	9	0.18	3.57 ± 0.34	0.28 ± 0.14
Cazorla					
Aphaenogaster iberica	13	10	0.77	1.62 ± 0.21	6.76 ± 1.55
Camponotus cruentatus	17	11	0.65	1.35 ± 0.17	4.59 ± 1.48
r/b Leptothorax	47	30	0.64	5.36 ± 0.51	0.23 ± 0.04
Pheidole pallidula	39	22	0.56	3.23 ± 0.48	0.21 ± 0.05
Plagiolepis pygmaea	30	8	0.27	3.97 ± 0.63	0.34 ± 0.09
Crematogaster sordidula	22	3	0.14	3.77 ± 0.58	NA

Table 4.4. Species-specific survival models, which include number of foragers in hoops and discovery temperature as covariates. These models resulted from model stepwise reductions. Where interactions are present, the main effects are presented, even if they are not significant. The value estimates for forager number correspond to the Per Capita Coefficient column of Table 4.2.

Species	Best Fit Model	Foragers		Temperature		Interaction	
		Coefficient	*P*	Coefficient	*P*	Coefficient	*P*
Doñana							
Aphaenogaster senilis	Foragers + Temp.	NA	0.000	0.07	0.001		
Crematogaster aubertii	Foragers	0.30 ± 0.09	0.001				
Plagiolepis pygmaea		NA	0.085				
r/b Myrmicine		NA	0.870				
Grazalema							
Aphaenogaster senilis	Foragers	0.77 ± 0.12	0.000				
Forelius sp.	Foragers	0.60 ± 0.15	0.000				
orange Leptothorax	Foragers + Temp. + Foragers x Temp.		0.160	-0.08	0.123	0.05	0.013
Crematogaster scutellaris		NA	0.090				
Plagiolepis pygmaea	Foragers	0.28 ± 0.14	0.040				
Cazorla							
Aphaenogaster iberica	Foragers + Temp. + Foragers x Temp.	NA	0.000	0.13	0.007	-0.17	0.000
Camponotus cruentatus	Foragers + Temp. + Foragers x Temp.	NA	0.002	0.13	0.019	-0.12	0.012
Crematogaster sordidula		NA	0.070				
Pheidole pallidula	Foragers	0.21 ± 0.05	0.000				
Plagiolepis pygmaea	Foragers	0.34 ± 0.09	0.000				
r/b Leptothorax	Foragers	0.23 ± 0.04	0.000				